Comparing Aquatic Communities across Spatial and Environmental Scales in the Mobile Bay Estuary

by

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Abstract

Estuaries are important ecosystems that sit at the interface of marine and freshwater environments. Mobile Bay is a large, river-influenced estuary in the northern Gulf of Mexico. The mechanisms that govern the variability in aquatic communities of this system are not well understood.

In Chapter 1, I quantified the fish and macroinvertebrate communities at 9 sites across a physical-chemical gradient. Species that could be used as indicators of the aquatic communities in the Mobile Bay were identified using multivariate methods. Salinity was found to be the most important environmental variable for structuring the aquatic communities, with dissolved oxygen and water temperature playing a secondary role. Seasonally, I found that aquatic communities showed the greatest differences across-sites during winter, probably due to migratory species spending part of their life history outside of the Mobile Bay.

In Chapter 2, I investigated how Largemouth Bass used the variable forage base in the Mobile Bay estuary. Multivariate methods were used to identify important prey types to 467 adult Largemouth Bass along a spatial and seasonal gradient. I found that macroinvertebrates were important to Largemouth Bass diets at all 3 study sites. The greatest variation occurred during the spring, when Gulf Menhaden and other migratory species became available to predation, particularly at sites downstream in the estuary.

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Introduction

Estuaries are transitional environments that occur at the interface between freshwater and marine ecosystems. These estuarine zones have received considerable attention due in part to their value as nursery areas for economically important fauna, water purification areas, and wave barriers (Dahlgren et al. 2006; Davis et al. 2012; Sheaves et al. 2013). Many estuaries are in close proximity to some of the largest human population centers and have endured significant environmental degradation (Courrat et al. 2009; Martino and Able 2003). Fish and macroinvertebrates within these systems have been identified as potential biological indicators (Marshall and Elliott 1998), for reasons that include: (1) fish and macroinvertebrates are relatively long lived, allowing variation in their abundances to be better compared with historic environmental data, (2) they are readily found in estuarine systems, and (3) their communities can include multiple trophic levels which can provide a more complete picture of the response to environmental gradients or anthropogenic disturbances (Whitfield and Elliott 2002).

Estuaries have been broadly defined as the area where freshwater rivers meet the sea (Ferguson et al. 2013; Harrison and Whitfield 2006). Ecologists have referred to estuaries as harsh zones with rapid variation in environmental variables that also contribute high biological productivity (Courrat et al. 2009; Martino and Able 2003). These systems are highly productive because of abundant food and high nutrient availability (Craig 2012; Nicolas et al. 2010). While many of these areas have received significant research attention, the complexity of the environment, combined with the high diversity of species, makes understanding the mechanisms determining the distribution of organisms within estuaries difficult.

Estuaries contain environmental gradients that can affect biological function across a large scale (e.g., variable climate) while other gradients are important on a more local spatial scale (e.g., tidal fluctuations) (Rakocinski et al. 1992). These conditions act as physiological filters, structuring the fish community based upon individual species' tolerances to abiotic factors (Martino and Able 2003). To live within estuaries, organisms are organized along these gradients in a way that allows them to survive and reproduce (Buchheister et al. 2013; Greenwood 2007; Lankford and Targett 1994; Peterson and Ross 1991).

The distribution of fish and macroinvertebrates in estuarine and coastal waters can be correlated with several abiotic factors (Deegan 1990; Kupschus and Tremain 2001; Whitfield 1999). Dissolved oxygen can play a role in organizing fish assemblages and macroinvertebrate communities with hypoxic events leading to emigration behavior in mobile species (Craig 2012; Langseth et al. 2014; Stevens et al. 2006). Ambient water temperature has been shown to affect distributions of fish in estuaries (Harrison and Whitfield 2006). Total fish abundance varied with temperature changes in the Humber Estuary, UK, by creating a barrier to fish movement due to thermal tolerances of species (Marshall and Elliott 1998). Habitat structure (e.g., marsh grass and vegetation) can also affect fish communities (Rashleigh et al. 2009; Wagner and Austin 1999), primarily by serving as a refuge from predation for small species and juvenile fish (Baltz et al. 1993). Species associations with different habitat types can sometimes play a role when explaining large scale patterns of community structure (Nicolas et al. 2010).

Salinity is also an important abiotic factor organizing fish and invertebrate communities within estuaries (Barletta et al. 2005; Harrison and Whitfield 2006; Peterson and Ross 1991;

Wagner and Austin 1999). This is particularly true when trying to explain patterns of community structure and biodiversity across an entire estuary (i.e., patterns of community organization across the entire Chesapeake Bay Estuary), (Lefcheck et al. 2014) as well as making comparisons between estuaries (i.e., comparisons of patterns across 6 European estuaries), (Mathieson et al. 2000). Adaptations that allow fishes to tolerate salinity extremes can determine their ability to occur in areas (Martino and Able 2003; Whitfield 1999). The salinity gradient and the resulting fish community can be affected by freshwater discharge from rivers (Ferguson et al. 2013; Gillson 2011; Gonzalez-Ortegon et al. 2012) as well as by tidal fluctuations, which can bring saltwater into estuaries and can also be correlated with influxes of marine species into estuarine areas (Marshall and Elliott 1998; Rountree and Able 1997). Tropical storms have been shown to introduce large amounts of salinity to estuaries in some instances (Park et al. 2007), or introducing large amounts freshwater from rainfall (Mallin et al. 2002). It appears that these effects from large storm events may be short lived and recovery is normally rapid for highly resilient estuarine communities (Lewis et al. 2011).

Biotic interactions and the effects they can have upon the fish community can vary due to differences in fish life history patterns, such as use of the estuary only at certain life stages (Sheaves et al. 2013). Juveniles of many fish and macroinvertebrate species use estuarine waters (Carassou et al. 2011; Harding and Mann 2001; Heck et al. 2001; Hernandez et al. 2010; Paterson and Whitfield 2000). For example in South Africa, temperate estuarine shallow water areas have been found to support high numbers of juvenile fishes (Paterson and Whitfield 2000). Predation risk can be lower in areas where juveniles can use habitat that is unavailable to piscivores (Brady and Targett 2013; Harrison and Whitfield 2006; Manderson et al. 2004). In contrast, a study in New Jersey found that large fishes can move into these shallow estuarine areas during changes in tidal direction which periodically increased predation risk (Rountree and Able 1997).

The Mobile Bay Estuary, Alabama, is a river-dominated system in the northern Gulf of Mexico (GoM). The salinity gradient in the system is influenced by freshwater inflow from the confluence of the Tombigbee and Mobile Rivers (Carassou et al. 2011). Previous work on fish distributions within the Mobile Bay has shown that water chemistry played a role in organizing fish communities (Rashleigh et al. 2009; Swingle and Bland 1974). Other studies have concluded that juvenile fish abundances in the system are heavily influenced by riverine processes (Carassou et al. 2011). Rozas et al (2013) found that nekton communities within the Mobile Bay estuary were driven by recruitment of young transient species, and greater hydrological connectivity to the bay improved the abundance of recruits. Results from previous work have also suggested that macroinvertebrate communities depend on vegetated areas of the Mobile Bay estuary for nursery grounds (Heck et al. 2001; Morgan et al. 1996). Largemouth Bass have been found to use upstream portions of the Mobile Bay estuary, and exhibit different life history patterns than freshwater populations (Farmer et al. 2013; Glover et al. 2013; Lowe et al. 2009; Norris et al. 2010). Movements of Southern Flounder indicate that they spend a portion of their life in the freshwater areas of the estuary (Farmer et al. 2013; Lowe et al. 2011). The results of previous work suggest that fish and macroinvertebrate assemblages may be defined by a salinity gradient. However, extensive work has not been conducted across the complete salinity gradient, connecting all salinity zones from oligohaline to euhaline.

The objectives of the present study were to (1) describe communities of fish and macroinvertebrates across the landscape scale of the Mobile Bay Estuary, (2) identify the dominant fish and macroinvertebrate species that defined those distinct communities, (3) determine which environmental variable(s) provided the greatest contribution to the explained variance in fish and macroinvertebrate community structure

Methods

Field Collection

Nine sites were sampled every other month in the Mobile Bay estuary (Figure 1; Table 1) from April 2011 – February 2015. Sites were selected to include the entire physiochemical gradient available to fish and macroinvertebrates in the estuary, but not all sites were sampled on every date, due to differences in study objectives across the various studies contributing to the dataset (Table 1). Collections only occurred at high tide and during daylight hours to minimize sampling variation. To minimize bias for comparing between sites, the Fowl River South (FRS) site was sampled first and the gear used there was then used at both the Fowl River North (FRN) and Fowl River (FR) sites for that sampling trip. Fish were collected with boom electrofishing and prod-pole electrofishing when salinities were <8 ppt (Peer et al. 2006). Boom electrofishing methods consisted of two 10-minute transects at each site with a boat operator and two netters. Prod-pole electrofishing targeted juveniles and small individuals, and was carried out by taking one 10-minute transect. The combined boom and prodpole-electrofishing transects yielded a total of 30-minutes of electrofishing effort at each site. All electrofishing was conducted at low voltage settings (170 DC) and high amps 18-20+. If salinity was >8 ppt, conductivity of the water would not allow electroshocking. Instead, two seine transects were conducted with a 9.1-m bag seine (4-mm mesh) to target small adult, sub-adult, and juvenile fish. Effort was standardized across sites by limiting each seine transect to 15 m in length. Seines were drawn by two individuals with a third individual holding down the lead line to minimize escapement under the seine.

Abiotic measurements were taken prior to each sampling event. A YSI model 30 meter was used to measure surface salinity (ppt) and water temperature (ºC) values and a YSI model 51B meter was used to collect surface dissolved oxygen measurements (mg/l). Secchi depth was measured prior to field collections.

Existing Data

Data were available from previous investigations in the Mobile-Tensaw Delta / Mobile Bay Estuary (Table 1). Collections were carried out monthly from February 2002-April 2009. These data include collections from Bay Minette (BM) and D’Olive Bay (DB), and the methods for fish and abiotic collection were the same as previously described, except that effort was greater. In the historical dataset, two 15-minute boat electrofishing transects three 10-minute prod pole electrofishing transects were taken, for a total of 1 hour of effort at each site on each sample date. The exception was during 2002, when no prod pole collections were taken.

Sample Processing

All fish and macroinvertebrates collected in electrofishing and seine transects were preserved and returned to the lab for processing. All individuals were identified to species. Length (mm) and wet weight (g) of all fish were taken and the uropod of shrimp and the carapace width of crabs were measured; when more than 20 individuals of a single species were collected the total biomass of each species was divided by the mean weight of a subsample (n=20) to obtain an estimate of total number.

Analysis

Separate ANOVA tests were used to test the null hypothesis that there were no differences in the measured environmental variables across sites and seasons. Because salinity values did not meet the assumptions of normality, salinity was log(x+1) transformed prior to analysis, which helped the response variable to better meet the assumptions of the linear model (Ellison and Gotelli 2004). Two salinity measurements and eighteen dissolved oxygen measurements were not taken due to equipment malfunction. Seasons were defined as: SPRING = March – May, SUMMER = June – August, FALL = September – November, WINTER = December – February. All ANOVA models were originally run with a site x season interaction included; however, no significant interactions were found so the interaction terms were removed. If a significant effect was identified, a Tukey's Honest Significance Difference post hoc test was used to compare group means.

A variety of descriptive statistics were used to assess differences in species composition in these data. From here on; "Samples" are defined as the total catch at each site, on a particular date. Species richness was defined as the number of species per sample and was tested for correlation with the three environmental variables by fitting generalized linear models (GLM), originally with all pairwise interaction terms included; however, it was determined that the interactions caused extreme variance inflation so the interactions were removed. A GLM model with Poisson errors was selected because species richness was quantified as count data and the observed distribution displayed the attributes of a Poisson distribution. A measure of community diversity was obtained using Simpson's index of diversity (Simpson 1949). The Shannon's-Diversity index value was calculated for each sample (H) and was divided by the logarithm of maximum species richness. The resulting Pielou's value (J) is a measure of species evenness

(Legendre and Legendre 2012; Pielou 1966). Both evenness and Simpson's diversity were tested for correlation with the measured environmental variables using separate linear regressions. Linear regressions were originally conducted with all pairwise interaction terms included; after determining that these terms were not statistically significant, they were removed and the analysis re-run.

A matrix of relative abundances was generated from species catch data. Species abundances were reported as catch-per-unit effort (CPUE) by dividing each sample by the number of transects from all gears pooled. The resulting *samples x species* matrix was used to compare the fish and macroinvertebrate community assemblage of the nine Mobile Bay Estuary sites. In order to reduce the effect of differences in effort and selectivity between gears, the data were relativized by the sample totals. This method of standardization is appropriate when considering samples that have unequal effort, or are collected with different units of measurement (McCune et al. 2002). The resulting matrix was used to compare proportional abundances of organisms within samples in species space.

A hierarchical cluster analysis was performed on a matrix of square root transformed, proportional fish abundances using the group average linkage method. The influence of rare species was minimized prior to analysis by removing species that appeared in fewer than 3% of samples (Martino and Able 2003; McCune et al. 2002). Hierarchical agglomerate clustering was used to group samples by site and by season based upon their distances in a Bray-Curtis similarity matrix. The group average linkage method was selected because of the compatibility of this method with Bray-Curtis similarity matrices (McCune et al. 2002). After initial clustering, two samples (i.e., one from Fowl River North and one from D' Olive Bay) were removed because they contained extremely low catches, a result of difficult sampling conditions (i.e., low water conditions did not allow for sampling the entire transect) so that the samples were not representative of the biological community, skewing the analyses (Lubinski et al. 2008).

Non-metric multidimensional scaling was selected as the method to display the results of the clustering routine. This method allows samples to be graphically compared to one another in a reduced number of dimensions (Legendre and Legendre 2012). A permutational multivariate analysis of variance model (PERMANOVA) was used on the Bray-Curtis distance matrix to test the null hypothesis of no differences among 3 groups of samples (cluster, site, season); sampling year was included as a blocking variable to remove variation across years (Anderson 2001; McCune et al. 2002). This method was chosen because it allows for the use of a non-euclidian distance matrix, such as Bray-Curtis, to test for differences in variation between groups of similarities (McCune et al. 2002). A similarity percentage analysis (SIMPER) was used to determine the species responsible for the differences observed between significant clusters of samples (Clarke 1993).

A method of direct gradient ordination was used to describe the effect of the collected environmental variables on aquatic community structure. Canonical correspondence analysis (CCA) was selected because it responds well to species that have unimodal responses to environmental gradients (McCune et al. 2002; Ter Braak 1987). In addition, the method is also useful when describing ecological situations where the mode of a species response is present along the environmental gradient (Legendre and Legendre 2012). CCA was conducted on the same transformed, proportional abundance data used in the previously described analyses. The resulting ordination is independent of variation that is not related to environmental variation (McCune et al. 2002).

Results

Environmental variation

Surface salinity ranged from 32.0 ppt (summer, 2012 at site PB) to 1 ppt (mean = 7.70; S.D. = 8.16) and differed across sites (F = 78.33; p <0.001). Results from Turkey's Honest Significance Difference test showed a clear gradient from the upstream to downstream portions of the estuary (Fig. 2). Although salinity differed significantly across seasons (Fig. 3) (F = 9.56; $p < 0.001$), only salinity in the spring differed from all other seasons ($p < 0.001$).

Dissolved oxygen reached a maximum of 16.4 mg/l (fall, 2012 at site FBA) and a minimum of 2.20 (spring, 2014 at site FRN) (mean = 8.01; S.D. = 2.22) and differed statistically across sites (Fig. 2) (F = 3.138; $p = 0.002$). Although no clear gradient could be observed, both of the furthest upstream sites (DB, BM) had significantly higher mean dissolved oxygen concentration versus the FRN site (BM: $p = 0.05$; DB: $p = 0.03$). Dissolved oxygen also differed significantly across seasons (Fig. 3) (F = 26.2; p <0.001), being highest in the spring and winter, intermediate in the fall, and lowest in the summer.

Mean water temperature ranged from 34.4 ^{0}C (summer, 2013 at site FBA) to 8.7 ^{0}C (winter, 2006 at site DB) (mean = 23.01; S.D. = 6.56), and did not differ across sites (Fig. 2). There were significant seasonal differences in mean water temperature (F = 521.8; p<0.001), being highest in the summer, followed by fall, spring, and winter (Fig.3).

Species richness, diversity, and evenness

The 317 samples from the combined datasets yielded 170,856 individuals from 133 identified species captured across all gear types. The 10 most abundant species in the study contributed over 1.5% of the total catch (Table 2).

Species richness in any particular sample ranged from 1 to 31 (mean = 12; S.D. = 6) (Table 3). The results of the GLM model produced two significant relationships (Table 4). For every 1 ppt increase in salinity the number of species decreased by 0.965 (95% C.I. = +/-0.01; *p* = <0.001) species, suggesting that samples taken at higher salinity would contain fewer species (Table 4). Secondly, we found that for every 1 ^{o}C increase in water temperature, species richness increased by 1.022 (95% C.I. = +/- 0.01; *p* = <0.001) (Table 4).

Linear regression analysis of Simpson's diversity index with the environmental variables produced two significant relationships (Table 4) (df = 293; R^2 = 0.25). For every 1 ppt increase in salinity, the probability that two organisms in a sample were different species decreased by 0.014 (95% C.I. = 0.01; *p* value = <0.001). Second, for every 1 ^{o}C increase in temperature, the probability that two organisms in a sample were different species increased by 0.007 (95% C.I. = +/- 0.01; *p* value = <0.001). Linear regression of species evenness showed one correlation with the environmental variables (Table 4) (df= 293; R^2= 0.13), decreasing 0.01 (95% C.I. = +/- 0.01; *p* value = <0.001) with every 1 ppt increase in salinity (Table 4).

Aquatic Community Analysis

The clustering analysis identified 5 clusters related to fish and macroinvertebrate community composition within the study area. The nMDS ordination (3D stress = 0.175) illustrated the separation between groups and supported the cluster classifications. The clusters of samples clearly separated based upon site location within the Mobile Bay estuary. Seasonality also played a role in separating the clustered groups of samples primarily during winter (Fig. 4). Similarity percentage analysis identified the important species that contributed the greatest effect on the changes within the Bray-Curtis similarity matrix. Only species that had >3% contribution to group dissimilarity were included.

These results were confirmed by the PERMANOVA model (Table 5). We found statistical differences among clusters generated by the previous analysis (df =4; F= 34.31; R^2 =0.262; *p* value = <0.001). We also found statistical differences existed among sample sites (df =8; F =7.06; R^2 =0.109; *p* = <0.001) and among seasons (df =3; F =8.27; R^2 =0.048; *p* value = <0.001). The R^2 values of the results suggest that our clustering result explained a greater amount of variation within the community data than did either the season or site factors independently. A secondary finding suggested that spatial variation across sites (R^2 =0.109) explained a greater amount of variation than did season (R^2 =0.048).

Cluster 1 was dominated by samples from the two main upstream sites (DB, BM) across all seasons. Pairwise comparisons of cluster 1 and the other clusters (Table 6) indicated that the community showed high proportional abundances of Bluegill (0.244), Redear Sunfish (0.232) Gulf Menhaden (0.212), Largemouth Bass (0.229), Redear Sunfish (0.232) and Spotted Gar (*Lepisosteus oculatus*) (0.159). Cluster 2 represented a different freshwater community and was dominated by samples from FRN across all seasons. The community composition showed higher proportional abundances of Largemouth Bass (0.431), Brook Silverside (0.413) and Redear Sunfish (0.158). Cluster 3 represented a coastal assemblage, with representative samples from four downstream sites (FR, FRS, FBB, WB and PB) across all seasons. The important species were Bay Anchovy (0.314), Inland Silverside (0.377), Spot (0.253) and Pinfish (0.208). Cluster 4 illustrated a shift in the coastal community during winter. Cluster 4 contained a greater number, relative to cluster 3, of the samples taken in the winter at four of the five coastal sites (FR, FRS, FBA and FBB); secondarily, this group was dominated by samples from FBA across all seasons. The winter group community consisted primarily of Dagger Blade Grass Shrimp (0.753), Gulf Killifish (0.126), and Sheepshead Minnow (0.126). Cluster 5 included five samples from winter across four sites (FBA, FBB, WB, and PB). This cluster represented a second winter assemblage, one dominated by sciaenids (0.786) and Striped Mullet (0.332).

The CCA model (based upon proportional abundance) identified two axes that explained a cumulative 90% of the species-environment variation (Table 7). The first CCA axis (CCA-1) had an eigenvalue of 0.34 and had a high positive loading of salinity with smaller, negative loadings of DO and temperature. Fourteen of the discriminatory species identified from the SIMPER routine were observed in the CCA model. The species with the greatest negative correlations with CCA-1 were Brook Silverside (-0.546), Bluegill (-0.528) Spotted Gar (-0.521), Largemouth Bass (-0.510), Redear Sunfish (-0.490) and Gulf Menhaden (-0.384) (Fig. 5a). Species that showed positive correlations with CCA-1 were sciaenid spp. (1.148), Dagger Blade Grass Shrimp (0.795), Gulf Killifish (0.692), Pinfish (0.676), Spot (0.594), Inland Silverside (0.446), Bay Anchovy (0.312), and Stripped Mullet (0.218). CCA-1 described a clear spatial salinity gradient of the communities from the nine sample sites (Fig. 5b). Positive correlations with the second axis in the CCA model (CCA-2) axis indicated species associations with warmer water temperatures (Table 7). Species with the greatest positive correlations along CCA-2 were Pinfish (0.570), Spotted Gar (0.273), Bay Anchovy (0.198) and Spot (0.133). In contrast, species associated with cooler temperatures held negative correlations with CCA-2. Of the 14 discriminatory species the greatest negative correlations with CCA-2 were Sciaenid spp. (-0.944), Dagger Blade Grasss Shrimp (-0.510), Gulf Killifish (-0.438), Largemouth Bass (-0.271), Redear Sunfish (-0.203), Gulf Menhaden (-0.133), Bluegill (-0.098), Stripped Mullet (-0.060), Brook Silverside (-0.033) and Inland Silverside (-0.017) (Fig. 5a). The second axis in the CCA model (CCA -2) illustrated a seasonal, water temperature gradient that discriminated among the coastal sites (Fig. 5b).

Discussion

The fish and macroinvertebrate assemblages of the Mobile Bay Estuary were structured by multiple factors. The effect of seasonality and environmental variation on fish and macroinvertebrates within estuarine systems have received research attention in other estuarine systems. However, in general these studies have been small in temporal scale (~1-3 years) and limited to considering only a part of the salinity gradient. Secondly this project is one of few in the northern Gulf of Mexico to address the fish and macroinvertebrate communities of estuaries east of the Mississippi River Delta.

Environmental gradients and diversity

The Mobile Bay estuary was home to a diverse aquatic community that varied both spatially and temporally, especially along the upstream-downstream gradient. My analysis found that overall species richness patterns were most strongly related to salinity and temperature suggesting that the number of species declined, or that my ability to sample effectively, was reduced during times of high salinity and colder water temperatures. Other studies conducted in estuarine systems have produced contrasting conclusions about general species richness patterns within estuaries (Akin et al. 2005). In New Jersey, researchers found that species richness increased towards the estuary mouth (Martino and Able 2003). Akin et al. (2005) found that species richness increased as geographic distance from the Medeteranian Sea decreased. Multiple authors have agreed that differences in observed patterns in general species richness across studies stem from differences in estuary catchment size (Whitfield 1999) or study differences in geographic scale (Akin et al. 2005; Martino and Able 2003) and local environments where sampling occurred (Martino and Able 2003). In my study it may be that the upper bounds of the study area are at the freshwater-saltwater interface for much of the year; if the study bounds were extended further upstream into the Mobile-Tensaw River Delta, a decrease in species richness might result. It has been noted that species richness can depend on sampling gear selectivity and the sampling effort (Selleslagh and Amara 2008; Warry et al. 2013); therefore it could be that differences in effort between the existing data and the current study created the observed pattern, because higher effort could capture more species.

Both Simpson's diversity index and community eveness were negatively related to salinity, and positively related to water temperature, supporting that areas in the upper portions of the Mobile Bay are areas of high diversity. This high diversity is driven by the interface of freshwater and marine species distributions. Other regional studies of estuarine species diversity have noted that diversity can be high in upstream areas. Peterson and Ross (1991) found that fish species and decopod species diversity were greater in tidally-influenced freshwater and oligohaline areas of coastal Mississippi than in mesohaline habitats. They concluded that this pattern was produced by the mixing of a large number of freshwater organisms with marine species. In Texas coastal wetlands, researchers found that overall fish species diversity was positively related to water temperature and water depth (Gelwick et al. 2001). The freshwater fish assemblages of the lower coastal plain of Alabama have a high number of fish species (Lydeard and Mayden 1995); this is one reason for why the estuaries of the north Gulf of Mexico show a pattern of high diversity in the upstream areas.

Biotic Community

Distinct fish and macroinvertebrate comunites were identified by the analyses. Assemblages in upstream sites of the estuary were dominated by centrachids, with influences from a few estuarine resident species. This finding is consistent with other studies of tidally influenced river deltas (van Vrancken and O'Connell 2010). Similarly, Gelwick et al. (2001) found that centrarchid species were likely to occur at salinities < 5 ppt, in a Texas estuary and were indicator species of upstream areas. In my study, Gulf Menhaden was an important component of the upstream assemblage and has been found to be abundant in Mobile Bay (Gregalis et al. 2009), particularly in spring and fall (Rozas et al. 2013). Deegan (1990) found Gulf Menhaden in Louisiana coastal areas used marsh creeks in the early part of the year, migrating to the open bay in late summer. My study supports the conclusion of Rozas et al. (2013) that upstream, low salinity, estuarine areas are critical habitat for Gulf Menhaden in the Mobile Bay Estuary.

The coastal areas of my study support a diverse assemblage of euryhaline organisms and marine species that varied seasonally. The differences in community composition in my study were primarily associated with winter versus other seasons, where high salinities and lower water temperatures may have caused species that could not tolerate extreme environments to move out of the area, coupled with a decrease in sampling effeciency. The absence of Bay Anchovy, Spot, and Pinfish in winter was an important characteristic of the seasonal community shift; all three species have been found to use areas outside of estuaries during winter (Currin et al. 1984; Nelson 1998; Nelson 2002; Vouglitois et al. 1987). Inland Silverside used estuarine waters year-round, though their disappearance from estuarine waters during winter has been documented in Florida estuaries (Middaugh and Hemmer 1992). The winter months of my study were characterized by three euryhaline, estuarine resident species (Gulf Killifish, Daggerblade Grass Shrimp, and Sheepshead Minnow) that spend their entire lives in shallow estuarine waters. Gulf Killifish have been shown to be abundant and express high site fidelity during summer in Mobile

Bay saltmarshes (Nelson et al. 2014); my findings similarly suggest that these organisms are persistent in the community year round. Estuarine community differences in winter have been found in other estuarine studies (Akin et al. 2005; Wingate and Secor 2008). Gregalis et al. (2009) showed low catch rates at shallow oyster reefs during winter in Mobile Bay. Similar findings in the Canche estuary (UK) found that winter fish assemblages were dominated by estuarine resident fishes (Selleslagh and Amara 2008).

The cluster analysis included in my study did not separate the Mobile Bay Estuary along an East-West spatial gradient. Separation of coastal fauna distributions has been proposed along the northern Gulf of Mexico coast, with some disagreement about where the zoogeographic boundary should be placed (Briggs 1974). My findings suggest that the prominent species of the estuarine communies are similar between east versus west sides of the bay. This result could be due to the dependence of coastal communities upon coastal processes (e.g., larval transport) (Martino and Able 2003). If the sampling were extended to better encompass the tributary watersheds of the Eastern portions of the estuary, then perhaps an east-west gradient in community might be more clearly demonstrated.

Community association with environmental variables

Upstream sites showed lower variability in community composition than downstream sites; similarly in the Chesapeake Bay where upstream, summer fish assemblages were more stable than fish assemblages in downstream mesohaline habitats (Wagner and Austin 1999). The observed pattern in variability could be attributed to differences in species tolerances to environmental variation. In the northern Gulf of Mexico, Peterson and Ross (1991) concluded that low salinity nekton was more tolerant to fluctuations in salinity and pH than were high salinity organisms.

I identified salinity as having the greatest impact on fish and macroinvertebrate community structure. Salinity has been similarly cited as important from other studies of estuarine systems (Barletta et al. 2005; Gelwick et al. 2001; Harrison and Whitfield 2006; Marshall and Elliott 1998). Salinity structures the aquatic community by removing species with low tolerances to hypertonic or hypotonic conditions. The effect of salinity on a species can vary with life stage (Marshall and Elliott 1998). Catch rates of Bay Anchovy at different life stages were found to vary with salinity (Peebles et al. 2007). In Medeterranian estuaries, the assemblage composition of five species of mullet were found to be related to the salinity preferences of juvenile mullet (Cardona et al. 2008). In this study, salinity was the most important variable for structuring communities across the upstream-downstream spatial gradient. This is consistent with other studies that have been conducted across large spatial scales (Akin et al. 2005; Harrison and Whitfield 2006; Marshall and Elliott 1998; Martino and Able 2003).

Temperature played a secondary role in structuring fish and macroinvertebrate communities. Marshall and Elliot (1998) noted that the thermal tolerances of individual species are rarely reached in the field and the effects of temperature are likely synergistic with other environmental factors. In my study the effects of temperature were likely acting as a surrogate for season, given that species with life history requirements outside of the estuary during times of low water temperatures were therefore not present in downstream areas during these times. Similarly seasonal patterns in abundance have been related to the large influxes of juveniles in estuarine areas, or spawning migrations of freshwater species upstream (Eick and Thiel 2014).

Dissolved oxygen (DO) had the least amount of influence on the estuarine aquatic community. DO in other studies affected aquatic communities primarily when hypoxic conditions were created, causing avoidance behaviors in some species (Craig 2012; Stevens et al.

2010). Many fish species become stressed at oxygen levels below < 4.5 ppm (Eick and Thiel 2014). However, in my study downstream sites were shallow and oxygen levels may never drop to low levels. The exception to this is the upstream site at Fowl River North; this site exhibited low oxygen levels likely a result of large amounts of detrital input. The result of low oxygen concentration was a community shift to species that tolerated this extreme environment, primarily Brook Silverside and Spotted Gar. The amount of river discharge can dramatically affect dissolved oxygen levels in upstream areas of estuarine systems (Mclusky and Elliott 2004). In Mobile Bay the amount of river influence from the Tombigbee and Alabama rivers may have maintained DO concentrations at tolerable levels in the upstream sites.

It is likely that other factors may have refined community structure of the Mobile Bay Estuary. Habitat complexity (as might influence substrate preferences) has been suggested in other studies to have an effect on the distributions of aquatic organims (Amara and Paul 2003). Martino and Able (2003) and Marshall and Elliott (1998) noted that other factors such as predator-prey interactions and distribution of food resources could also have an effect on the estuarine nektonic communities. These effects would be superimposed on the species responses to environmental variation that create the patterns of distribution within estuaries.

My results provide information about the seasonal and spatial variation in communities that should be incorporated into long-term monitoring programs. Estuarine research has focused on using fish and macroinvertebrate communities to evaluate environmental degradation (Mclusky and Elliott 2004; Partyka and Peterson 2008). My research has highlighted any monitoring effort would require consistent sampling across a long time series that is inclusive of the entire abiotic gradient available to fish and macroinvertebrates. Results of this study also highlight regional research needs in estuaries along the northern Gulf of Mexico. Specifically, a better understanding of individual species' responses to environmental variation, coupled with my results, would improve effectiveness of aquatic monitoring projects, both within the Mobile Bay. A better understanding of the life history of many of these species would similarly improve interpretations of these results; and our understanding of how aquatic communities in the northern Gulf of Meixco vary seasonally.

II. Comparisons of Coastal Largemouth Bass (*Micropterus salmoides*) Diets across Space and Time in Mobile Bay, Alabama

Introduction

Predator-prey interactions can play an important role in the life history of an organism (Diana 1995). Survival rate of predatory species can be associated with their ability to find prey efficiently, while minimizing their own risk of predation (Schoener 1971; Werner and Gilliam 1984; Werner et al. 1983). Condition and growth of predacious species are influenced by caloric intake gained from captured prey items (Glover et al. 2013; Yako et al. 2000). Simultaneously ambient environmental conditions can have an effect on energy lost while acquiring prey items (Krohn et al. 1997). A predator may have the ability to feed on a large diversity of organisms, but prey selection can be influenced by a combination of the density and abundance of the forage community and by predator preference (Krohn et al. 1997; Trippel et al. 2015). Because abundances of organisms at lower trophic levels can be variable (Livingston et al. 1997), it is important to understand the dynamics of how predators use resources both spatially and temporally.

In estuarine areas, abiotic conditions have been shown to influence the large-scale distribution of aquatic organisms (Barletta et al. 2005; Martino and Able 2003). Variation in how organisms distribute themselves within estuaries is a product of abiotic gradients, particularly salinity, which can influence community structure both spatially and seasonally (Buchheister et al. 2013; Carassou et al. 2011; Chadwick and Feminella 2001). Biotic interactions, such as predation, can act as a secondary filter, further refining macroinvertebrate and fish community structure along a salinity gradient (Boucek and Rehage 2013). During these interactions predators are presented with a diversity of potential prey species (Buchheister and Latour 2015; Wagner and Austin 1999). The high diversity of prey types is regulated by an interface of marine-derived, freshwater, and estuarine sources (Odum et al. 1979; Peer et al. 2006). Subsidy from marine sources may play a critical role in the growth and survival of coastal consumers (Boucek and Rehage 2013; Trippel et al. 2015).

Centrarchids are a prominent component of the fish assemblage in the oligohaline portion of many estuaries along the Gulf of Mexico (Glover et al. 2013; Norris et al. 2010; Peterson and Ross 1991; Stevens et al. 2013). Sunfish are important consumers within the food webs of these systems (Boucek and Rehage 2013; Peterson et al. 2006). Centrarchids are typically considered generalist predators and typically have diverse diets (Boucek and Rehage 2013; Boucek and Rehage 2014). Because of their role in coastal food webs, using these organisms as an ‘auto sampler’ has been explored, as a detection tool for exotic fauna or as a measure of changes in community composition (Boucek and Rehage 2014; Link 2004; Stevens et al. 2010). Largemouth bass diets have also been investigated as a detection tool for extremely rare species (Adams et al. 2015).

Largemouth Bass (*Micropterus salmoides*) in particular, is typically considered to be a stenohaline fish, although they can use oligohaline and mesohaline areas in estuaries (Lowe et al. 2009; Norris et al. 2010). Coastal Largemouth Bass populations can support abundant and active recreational fisheries, although large individuals are uncommon (Meador and Kelso 1990; Norris et al. 2010). An explanation of the lack of large individuals is that coastal Largemouth Bass have added energetic costs for osmoregulatory performance due to the influence of salinity (Glover et al. 2013). To offset these costs, Largemouth Bass in these areas may use seasonal prey provided by marine subsidies. For example in the St. Johns River, Florida, Largemouth Bass diets shifted during September through November to include a higher proportion of Atlantic Menhaden (*Brevoortia tyrannus*). In Mobile Bay, Alabama growth of first-year Largemouth Bass was found to be greater in downstream sites, where proximity to marine subsidies provided energy rich prey (Peer et al. 2006). Quantifying how adult Largemouth Bass resource use shifts seasonally and spatially may be important for understanding the life history and growth patterns of coastal populations of this species. For this study, I identified two research objectives: (1) to assess differences along a spatial gradient in the diet composition and niche breadth of adult Largemouth Bass and (2) to evaluate the impact of seasonality.

Methods

Study Area

Mobile Bay is a river-dominated estuary in the Northern Gulf of Mexico with the Tombigbee and Alabama rivers providing a large amount (~95%) of freshwater discharge into the bay (Johnson et al. 2002). The seasonality and timing of this discharge governs the magnitude of salinity intrusion into the upper portions of the estuary (Swingle 1971). During periods of low discharge, salinity can encroach into the Mobile River and influence the structure of macroinvertebrate assemblages (Chadwick and Feminella 2001). Fish and nekton communities can also vary both spatially and seasonally within the estuary (Rozas et al. 2013).

Three sites were selected to characterize a range of habitats and associated prey bases available to Largemouth Bass across seasonal and spatial gradients. Two sites (Bay Minette, D' Olive Bay) represented upstream sites; these sites were shallow, typically oligohaline bays characterized by low salinities with seasonal increases corresponding to salt wedge intrusion (Lowe et al. 2009). The third site was in the Fowl River, a tidally influenced river system that flows into the Mobile Bay (Figure 1). Salinity values were recorded just below the surface at the beginning of each bimonthly sampling event.

Fish Collections

Largemouth Bass were sampled every other month using pulsed-DC electrofishing (Smith-Root Model 7.5 GPP, 7,500 W; Smith-Root, Vancouver, Washington) or seine (bag seine: 9.1 m length, 4 mm mesh) from April 2011 – March 2015. All collected fish were weighed (g) and measured Total Length (TL) (mm). During each sampling event, ten individuals per site were euthanized, preserved on ice, and brought to laboratory where their diets were removed via dissection and preserved in 95% ethanol solution. The diets of all other captured Largemouth Bass were removed using acrylic tubes prior to release (Van Den Avyle and Roussel 1980); diet contents were placed immediately on ice and transplanted to the lab where they were stored frozen.

Stomach Content Analysis

Prey items from Largemouth Bass stomachs were identified to the lowest possible taxonomic level using dichotomous keys and otolith keys. A subsample of 10 individuals from each prey type were measured by taking the TL of fish (or otolith width for partially digested prey fish), carapace width of crabs, uropod length of shrimp species, and TL or head width for insects. Regressions from published literature (Benke et al. 1999; Culver et al. 1985; Dawson 1965; Smock 1980) and from my own samples were used to estimate prey weight, so that proportion by weight of each prey category to an individual bass' diet could be calculated (Storck 1986).

Statistical analysis

Descriptive statistics of diet richness (the number of prey types found in the stomach) and diversity (Shannon's diversity index,H') were calculated for each individual and averaged across individuals within both seasons and sites. Seasons were defined as: Fall = October, spring = March - April, summer = June - August, winter = December – February. Prey were identified to species for fish and invertebrate prey and to order for insects. Neither Shannon's diversity index nor species richness satisfied the normality assumption required for ANOVA, even after transformations were attempted; therefore separate Kruskal-Wallis tests were used to compare Largemouth Bass across seasons and across sites. This analysis has been used as an index of the width of the realized niche of an organism (Marshall and Elliott 1997). Where there were significant differences between sites or seasons, I used a pairwise multiple comparison of mean ranks (PMCMR) as a post-hoc test to identify which groups of diets were influencing the observed differences.

To compare Largemouth Bass diets between downstream and upstream sites, a %PCA ordination was performed on 19 prey categories representing those found in >1% of Largemouth Bass diets (Table 8). Only diets that had at least one of these 19 prey items in their stomach were analyzed (n=425). An *individual x prey category* matrix was formed where each row represented an individual bass diet, each column a prey category, and the elements represented the $\%W$ contribution of the prey category. The rows of this matrix were standardized to 1 (i.e. 100%) (De Crespin De Billy et al. 2000), and very small values (0.00001) were entered for zero and near zero elements to reduce the arch effect associated with some PCA structures (Aitchison 1983). The value of this method is that it allows individual fish and their prey types to be examined upon the same graph and secondarily allows the important prey types to be identified for future analysis through dimensional reduction.

For visual representation of seasonal variation in feeding strategy, Costello graphics were generated by plotting the total weight consumed (g) against the frequency of occurrence within the diets of each season (Costello 1990; Guy and Brown 2007). Finally, graphs depicting the average proportional weight of diets across season and site were generated to assess the average contribution of each prey category to diets from season and site simultaneously. Statistical analyses were performed in R version 3.1.3 using the package 'Vegan'; pairwise multiple comparison of mean ranks was conducted using the package 'PMCMR.'

Results

The five numerically most abundant prey types were Mysid Shrimp (*Mysidopsis spp.*), Gulf Menhaden (*Brevoortia patronus*), Blue Crab (*Callinectus sapidus*), Salt Marsh Mud Crab (*Panopeus spp.*), and Grass Shrimp (*Palaemonetes spp*.). Gulf Menhaden in diets were assumed to be *B. patronus* given that Yellowfin Menhaden (*B. smithi*) are rare within the Mobile Bay system (Anderson and Karel, 2007).

Niche breadth and descriptive statistics

Bi-monthly salinity measurements showed that all three sample sites were highly variable. Spatially, Fowl River had consistently higher salinities than both D'Olive Bay and Bay Minette, while late summer/early fall salinities were higher in D' Olive Bay than in Bay Minette (Figure 7). Largemouth Bass ranged in size from 93 - 445 mm TL. Visual comparision of Length-frequency histograms indicated that the sampled populations contained fish of similar sizes (Figure 8). Bay Minette sampling yielded the greatest number of individuals while D' Olive Bay and Fowl River contained similar sample sizes (Table 9). In the univariate analysis, 467 fish were included with 51 total prey categories (Table 9). Shannon's diversity index ranged from 0-1.36 (mean=0.765; SD=0.245). Values were highest during spring and at Fowl River (Figure 9).

Diet richness ranged from 1 to 6 prey types (mean=2.4; SD=0.794) and was generally higher during spring and at Fowl River (Figure 9).

The non-parametric Kruskal-Wallis test indicated that there were no significant differences in Shannon's diversity index across seasons (X^2 =3.0571; p value =0.3829) (Table 10; Figure 9). Diversity did differ significantly across sites (X^2 =15.4706; p value =<0.001) (Table 10; Figure 9). A pairwise multiple comparison test showed that Bay Minette and D' Olive Bay had similar diet diversity (p value =0.91) while Fowl River had a significantly higher Shannon's diversity index than Bay Minette (p value =<0.001) and D' Olive Bay (p value =0.01) (Table 10; Figure 9).

The global Kruskal-Wallis test of diet species richness did not differ significantly across season (Figure10) (X^2 =5.86; p value =0.330). Diet species richness did differ significantly across sample sites (X^2 =18.8503; p value =<0.001). A Pairwise multiple comparison test showed that Bay Minette and D' Olive Bay had similar diet species richness (p value =0.975),While being higher at Fowl River than both Bay Minette (p value =<0.001) and D' Olive Bay (p value =0.002) (Table 10).

Multivariate analysis of diet data

The first four axes of the %PCA analysis explained a cumulative 68.9% of the variance available within these data (Table 11). The ordination structure of the biplot points (Figure 11-12) exhibited the typical triangular structure of %PCA analysis (De Crespin De Billy et al. 2000). Data points clustered along the extremes of the variable arrows indicate dominance of that prey type. Prey types clustered towards the middle of the ordination were considered rare (De Crespin De Billy et al. 2000; Guy and Brown 2007).

The first axis of the %PCA ordination explained 27.1% of the total variation and showed the greatest correlation with Blue Crab (-0.928) (Figure 11A; Table 11). Overlays of mean site centroids along this axis showed overlap from all 3 study sites, indicating that Largemouth Bass from all sites consumed Blue Crab (Figure 11B). The second axis of the %PCA ordination explained another 16.8% of the total variation available within the dataset, and this axis was highly correlated with Salt Marsh Mud Crab (-0.877) (Figure 11A; Table 11). Mean site centroids along this axis showed overlap of Bay Minette and Fowl River but less overlap with D’Olive Bay; this indicated that fish from Bay Minette and Fowl River consistently consumed this prey type, while fish from D’Olive Bay did not (Figure 11B).

The third axis of the %PCA ordination explained 13.2% of the remaining variation within the dataset, and the greatest correlation was a positive association with Gulf Menhaden (0.705) and a negative association with Grass Shrimp (-0.703) (Figure 7A; Table 11). Overlap of Mean site centroids along this axis indicated that Gulf Menhaden were important to the diets of fish from all 3 study sites (Figure 12B). Similarly, overlap of mean site centroids indicated that fish from all 3 sites consumed Grass Shrimp (Figure 12B). The fourth axis of the %PCA explained 11.8% of the total variation within the dataset, the greatest correlation was with Mysid Shrimp (0.803) (Figure 12A; Table 11). Mean site scores along this axis indicated that Mysid Shrimp were found primarily in diets taken from Bay Minette fish (Figure 12B).

Predation strategy and spatial/temporal variation

Graphical interpretations taken from fish pooled within seasons indicated that Largemouth Bass from coastal AL estuaries are typically generalist predators that show high frequency and total consumption of invertebrate prey across all seasons (Figure 13-14). Fall Largemouth Bass diets were found to be the most variable, showing high frequency of occurrence across multiple species coupled with low total consumption, indicating high variation between individual feeding strategies (Figure 13). Spring Largemouth Bass had more specialized diets, with high total consumption of two invertebrates, Blue Crab and Salt Marsh Mud Crab. Spring fish also showed higher frequency of occurrence and total consumption of Gulf Menhaden than in other seasons (Figure 13). Summer Largemouth Bass appeared to specialize on invertebrates, particularly Blue Crab (Figure 14). Winter Largemouth Bass had a mixed feeding strategy, showing a much larger selection for sunfishes and mysid shrimp prey than in other seasons (Figure 14).

Graphical display of average proportional weight across sample sites and season confirmed the results of the %PCA analysis in that fish from all sites used invertebrate prey types regardless of season (Figure 15). Fish from Bay Minette appeared to consume the greatest amount of sunfishes, particularly in the winter. Fish from D' Olive Bay consumed the least amount of Salt Marsh Mud Crab while consuming a large amount of Gulf Menhaden and Inland Silverside, particularly in the spring. Fish from Fowl River consumed a large amount of Gulf Menhaden in the spring, while also consuming a large proportion of rare prey types, typically Spot, Gulf Killifish and Stripped Mullet. Though it would appear as though winter fish from D' Olive Bay and fall fish from Fowl River consumed entirely macroinvertebrate prey, those results are based on extremely low numbers of diets (n=2 and n=1 respectively) (Figure 15).

Discussion

This study focused on patterns of prey consumed by coastal Largemouth Bass. Past studies in estuarine systems have attributed growth patterns in Largemouth Bass to consumption of macroinvertebrates, coupled with energetic costs associated with life along a salinity gradient

(Glover et al. 2013). In my study, the most dominant prey types, both in terms of frequency and numerical abundance, were macroinvertebrates; disentangling the seasonal and spatial dynamics of diet composition can provide an understanding of how these predators use resources during the course of their life.

Largemouth Bass captured during this study were all adult fish and were able to consume a large number of prey types. In other estuarine studies Largemouth Bass have been found to function as generalist predators, feeding on invertebrate and fish prey from both marine and freshwater sources (Boucek and Rehage 2013; Peterson et al. 2006). In South Africa, Largemouth Bass fed on both estuarine finfish and invertebrates (Wasserman et al. 2011). In my study, we found a total of 51 prey types in Largemouth Bass diets, supporting the previous findings that Largemouth Bass are able to consume many of the prey types available within the estuarine system.

Diet diversity and niche breadth increased along a gradient from upstream to downstream sites, suggesting that fish at downstream sites consumed a greater number of prey types. Findings from fish community analyses have shown that estuaries typically have high diversity of species near the mouth (Akin et al. 2005; Martino and Able 2003). Our results indicate that this is due to the increase of marine subsidy, such as anadromous migration of marine species or estuarine habitats functioning as nursery grounds for prey species. Studies on Largemouth Bass from other estuaries have suggested that these fish have an increased potential to prey upon marine migratory species that use tidal rivers as nursery areas (Wasserman et al. 2011).

Macroinvertebrate species, particularly Blue Crab and Salt Marsh Mud Crab, were found in our study to consistently dominate the diets of Largemouth Bass. Similarly, Norris et al. (2010) found that Blue Crab were consistently the dominant prey type found in Largemouth Bass from the Mobile-Tensaw delta (Norris et al. 2010). Mobile Bay estuary has been cited as having a high abundance of Blue Crabs, even when compared to estuaries of the Atlantic coast estuaries, probably due to the warmer climate (Morgan et al. 1996). Results from my study suggest that Largemouth Bass in Mobile Bay select for macroinvertebrate prey, supporting other findings that have reported high consumption rates of macroinvertebrates by Largemouth Bass in estuaries (Boucek and Rehage 2013; Wasserman et al. 2011).

The seasonal trend of high macroinvertebrate consumption did appear to be variable, given that spring diets at both Fowl River and D' Olive Bay showed much higher consumption rates of estuarine migrant Gulf Menhaden than in other seasons. It has been shown that anadromous clupeid prey were important contributers to diet and simulated growth and condition of Largemouth Bass in Atlantic coastal systems (Yako et al. 2000). Juvenile Gulf Menhaden have been shown to spend spring and early summer in marsh creek areas before migrating to the open bay during fall (Deegan 1990). In Mobile Bay, it has been shown that Gulf Menhaden used oligohaline areas of the system as nursery grounds (Rozas et al. 2013). In our study it would appear that this nursery function provides seasonal prey opportunity for Largemouth Bass, particularly in downstream areas with direct connectivity to the Gulf of Mexico. It is important to note that no Gulf Menhaden appeared in the Largemouth Bass diets from Bay Minette during the spring and only in small proportions during summer; this could be because this site is upstream in the estuary and has the lowest amount of salinity influence. Alternatively the US Highway 90-98 causeway crosses the Mobile Bay just below the Bay Minette study site. Rozas et al. (2013) found that Gulf Menhaden were rare in nekton samples from above this causeway, and it could be that the development of the causeway acts as a barrier to Gulf Menhaden movement into the upper estuary.

Another surprising finding in our study was that winter Largemouth Bass diets from Bay Minette were dominated by sunfish species. In Florida, one study concluded that periods of marsh drying removed habitat that was previously used by marsh fish for refuge from Largemouth Bass and Bowfin (Boucek and Rehage 2013). In Mobile Bay, water levels are typically low during winter, possibly creating a situation where sunfish are forced out of the vegetated refuge areas, allowing for increased rates of predation by Largemouth Bass. Alternatively, an explanation could be that Blue Crab migrated away from this area of the Delta during this season (Morgan et al. 1996), allowing for a situation where Largemouth Bass were forced to feed on alternative prey types due to low abundance. Clearly the mechanisms responsible for the variable diets that we observed require additional research.

In conclusion, my study quantified the important prey resources to Largemouth Bass within coastal systems. My data provide information about the seasonal variation in resource use by Largemouth Bass, but cannot evaluate the effect of the causeway on the ability of marine prey species to move into the upstream areas of the Mobile Bay. In tidally influenced river systems, such as Fowl River, where large spring pulses of marine subsidy occur, it could be that Largemouth Bass receive a larger amount of their forage from marine subsidies than was previously thought. For broader perspective, the ability of Largemouth Bass use abundant macroinvertebrate prey, as well as seasonal marine subsidies may allow them to persist in areas where more specialized predators would have been extirpated.

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Table 1: A description of the multiple datasets included in the study, including the number of sampling events taken at each site and these dates (a "+" indicates that that a site was sampled for fish and macroinvertebrates). Site abbreviations are in parentheses.

Site	# samples	Jan, 2002 – Apr, 2009	Apr, 2011 – Aug, 2011	Oct, 2011 – Feb, 2014	Apr, 2014 – Feb, 2015
Bay Minette (BM)	99	+		+	+
D’ Olive Bay (DB)	88	+	+	+	+
Fowl River North (FRN)	6				+
Fowl River (FR)	24		+	+	+
Fowl River South (FRS)	6				+
Fowl Bay A (FBA)	23		+	+	+
Fowl Bay B (FBB)	23		+	+	+
Wolf Bay (WB)	24				
Perdido Bay (PB)	24		+	+	+

Table 2: Summary of all species ranked by percentage of total catch, with a frequency > 3 % across all samples including, group, common name, scientific name, total catch, and percent of total catch (% total) from 9 sites within the Mobile Bay estuary.

Group	Common Name	Scientific Name	Total Catch	% Total
Teleost Fishes				
	Gulf Menhaden	*Brevoortia patronus*	51,412	30.091
	Bay Anchovy	*Anchoa mitchilli*	14,733	8.623
	Inland Silverside	*Menidia beryllina*	8,988	5.261
	Spot	*Leiostomus xanthurus*	8,470	4.957
	Sciaenid	*Scaenidae spp.*	7,407	4.335
	Mullet	*Mugil spp.*	3,558	2.082
	Bluegill	*Lepomis macrochirus*	3,091	1.809
	Redear Sunfish	*Lepomis microlophus*	2,701	1.581
	Largemouth Bass	*Micropterus salmoides*	2,620	1.533
	Silverside Shiner	*Notropis candidus*	2,583	1.512
	Redspotted Sunfish	*Lepomis miniatus*	1,759	1.030
	Stripped Mullet	*Mugil cephalus*	1,714	1.003
	Pinfish	*Lagodon rhomboides*	1,510	0.884
	Spotted Gar	*Lepisosteus oculatus*	1,085	0.635
	Threadfin Shad	*Dorosoma petenense*	745	0.436
	Warmouth Sunfish	*Lepomis gulosus*	739	0.433
	Gulf Killifish	*Fundulus grandis*	691	0.404
	Rainwater Killifish	*Lucania parva*	683	0.400
	Speckled Trout	*Cynoscion nebulosus*	417	0.244
	Weedshiner	*Notropis texanus*	397	0.232
	Silver Perch	*Bairdiella chrysoura*	384	0.225
	Skipjack herring	*Alosa chrysochloris*	355	0.208
	Brook Silverside	*Labidesthes sicculus*	342	0.200
	Sheepshead Minnow	*Cyprinodon variegatus*	324	0.190
	Black Crappie	*Pomoxis nigromaculatus*	290	0.170
	Golden Shiner	*Notemigonus crysoleucas*	289	0.169
	Red Drum	*Sciaenops ocellata*	217	0.127
	Atlantic Needlefish	*Strongylura marina*	200	0.117
	Atlantic Croaker	*Micropagonias undulatus*	200	0.117
	Longnose Killifish	*Fundulus similis*	196	0.115
	Chain Pickerel	*Esox niger*	182	0.107
	Saltmarsh Topminnow	*Fundulus jenkinsi*	156	0.091
	Gizzard Shad	*Dorosoma cepedianum*	145	0.085
	Southern Flounder	*Paralichthys lethostigma*	128	0.075
	Coastal Shiner	*Notropis petersoni*	114	0.067
	Striped Anchovy	*Anchoa hepsetus*	107	0.063

	American Eel	*Anguilla rostrata*	105	0.061
	Sheepshead	*Archosargus probatocephalus*	103	0.060
	Freshwater Goby	*Ctenogobius shufeldti*	101	0.059
	Yellow Bass	*Morone mississippiensis*	94	0.055
	White Mullet	*Mugil curema*	82	0.048
Group	Common Name	Scientific Name	Total Catch	% Total
	Channel Catfish	*Ictalurus punctatus*	80	0.047
	Tidewater Mojarra	*Eucinostomus harengulus*	70	0.041
	Leather Jacket	*Oligoplites saurus*	69	0.040
	Bay Whiff	*Citharichthys spilopterus*	65	0.038
	Freshwater Drum	*Aplodinotus grunniens*	64	0.037
	Hardhead Catfish	*Ariopsis felis*	63	0.037
	Sand Seatrout	*Cynoscion arenarius*	62	0.036
	Buffalo	*Ictiobus spp.*	59	0.035
	Sharptail Goby	*Gobionellus oceanicus*	59	0.035
	Bowfin	*Amia calva*	58	0.034
	Spotfin Mojarra	*Eucinostomus argenteus*	57	0.033
	Code Goby	*Gobisoma robustum*	54	0.032
	Naked Goby	*Gobisoma bosci*	53	0.031
	Least puffer	*Sphoeroides parvus*	48	0.028
	Darter Goby	*Ctenogobius boleosoma*	47	0.028
	Bayou Topminnow	*Fundulus nottii*	45	0.026
	Western Mosquitofish	*Gambusia affinis*	44	0.026
	Rough Silverside	*Membras martinica*	41	0.024
	Hogchoker	*Trinectes maculatus*	30	0.018
	Pipefish	*Syngthanidae spp.*	28	0.016
	Inshore Lizardfish	*Synodus foetens*	28	0.016
	Longnose Gar	*Lepisosteus osseus*	25	0.015
	Aligator Gar	*Atractosteus spathula*	24	0.014
	Chain pipefish	*Syngnathus louisianae*	21	0.012
	Common Carp	*Cyprinus carpio*	17	0.010
	Golden Topminnow	*Fundulus chrysotus*	15	0.009
	Blue Catfish	*Ictalurus furcatus*	14	0.008
Decapod Crustaceans				
	Daggerblade Grass Shrimp	*Palaemonetes pugio*	34,488	20.185
	White Shrimp	*Litopenaeus setiferus*	3,580	2.095
	Brown shrimp	*farfantepenaeus aztecus*	1,388	0.812
	Blue Crab	*Callinectes sapidus*	584	0.342
Gastropod Mollusk				
	Neritina	*Neritina spp.*	894	0.523

Table 3: Species richness, Simpson’s diversity index, and evenness values for all 317 samples taken in the Mobile Bay Estuary, Alabama. Mean species richness (S) was defined as the number of species present/sampling event. Simpson’s diversity index and Pielou’s evenness (J) were averaged across all samples.

Measure	Mean	Maximum	Minimum	SD
Species richness	12	31	1	6
Simpson's index	0.64	0.92	0.01	0.24
Evenness	0.63	1.00	0.02	0.23

Table 4: Table showing the formula, model type, independent variables, the relationship, the slope, 95% confidence interval and the *p* value for three models testing descriptive community measures against environmental variables. An “*” indicates significance at α = 0.05.

Model	Model/Independent Variable	Relationship	Slope	95% CI	p value
Species richness ~ Salinity + Dissolved Oxygen + Temperature	Poisson Model (GLM)				
	Salinity	-	0.965	0.01	< 0.001*
	Dissolved Oxygen	+	1.005	0.03	0.531
	Temperature	+	1.022	0.01	< 0.001*
Simpson's diversity ~ Salinity + Dissolved Oxygen + Temperature	Linear Regression				
	Salinity	-	0.014	0.01	< 0.001*
	Dissolved Oxygen	-	0.001	0.02	0.914
	Temperature	+	0.007	0.01	< 0.001*
Pielou's J ~ Salinity + Dissolved Oxygen + Temperature	Linear Regression				
	Salinity	-	0.010	0.01	< 0.001*
	Dissolved Oxygen	-	0.009	0.02	0.173
	Temperature	+	0.003	0.01	0.180

Table 5: Results of the PERMANOVA model (significance was $\alpha = 0.05$). The PERMANOVA test was stratified by year.

Factor	DF	F	R^2	*p* value
Cluster	4	34.31	0.262	0.001*
Site	8	7.06	0.109	0.001*
Season	3	8.27	0.048	0.001*
Residuals	299		0.578	
Total	314			

Table 6: Output from the similarity percentage routine (SIMPER) showing key contributions to the dissimilarity between assemblages. Avg. A is the average proportional CPUE for each species in the first group. Avg. B provides the same information for the second group. Contribution is the overall contribution of a species to the dissimilarity between the groups being compared.

Comparison	Total dissimilarity	Species	Avg. A	Avg. B	Contribution
Cluster 1 vs 2	83.8	Brook Silverside	0.014	0.413	8.729
		Largemouth Bass	0.229	0.431	6.55
		Redear Sunfish	0.232	0.158	5.279
		Gulf Menhaden	0.212	0	4.879
		Bluegill	0.244	0.14	4.809
		Inland Silverside	0.182	0.03	3.659
		Spotted Gar	0.159	0	3.194
		Redspotted Sunfish	0.15	0.054	3.055
Cluster 1 vs 3	85.9	Bay Anchovy	0.127	0.314	6.431
		Inland Silverside	0.182	0.377	6.352
		Spot	0.074	0.253	5.163
		Gulf Menhaden	0.212	0.029	4.811
		Bluegill	0.244	0.011	4.616
		Largemouth Bass	0.229	0.039	4.575
		Redear Sunfish	0.232	0.01	4.498
		Pinfish	0.027	0.208	4.008
		Unidentified Mojarra	0.047	0.124	3.134
		Spotted Gar	0.159	0.01	3.044
Cluster 1 vs 4	90.6	Daggerblade Grass Shrimp	0.064	0.753	14.809
		Gulf Menhaden	0.212	0.021	5.011
		Bluegill	0.244	0	4.844
		Redear Sunfish	0.232	0	4.702
		Largemouth Bass	0.229	0.006	4.694
		Bay Anchovy	0.127	0.134	3.809
		Inland Silverside	0.182	0.122	3.785
		Spotted Gar	0.159	0	3.179
Cluster 1 vs 5	93.8	Unidentified Sciaenid	0.002	0.786	17.507
		Stripped Mullet	0.068	0.332	6.742
		Gulf Menhaden	0.212	0	5.08
		Bluegill	0.244	0	5.034
		Largemouth Bass	0.229	0	4.934
		Redear Sunfish	0.232	0	4.891

Comparison	Total dissimilarity	Species	Avg. A	Avg. B	Contribution
		Pinfish	0.027	0.183	3.8
		Inland Silverside	0.182	0.057	3.477
		Spotted Gar	0.159	0	3.304
		Redspotted Sunfish	0.15	0	3.048
Cluster 2 vs 3	96.2	Largemouth Bass	0.431	0.039	10.74
		Brook Silverside	0.413	0	10.631
		Inland Silverside	0.03	0.377	9.482
		Bay Anchovy	0	0.314	8.029
		Spot	0	0.253	6.331
		Pinfish	0	0.208	5.103
		Redear Sunfish	0.158	0.01	4.154
		Bluegill	0.14	0.011	3.599
Cluster 2 vs 4	96.6	Daggerblade Grass Shrimp	0.021	0.753	19.975
		Largemouth Bass	0.431	0.006	11.63
		Brook Silverside	0.413	0	11.087
		Redear Sunfish	0.158	0	4.266
		Gulf Killifish	0.064	0.126	4.234
		Bluegill Sunfish	0.14	0	3.716
		Sheepshead Minnow	0.021	0.126	3.582
		Inland Silverside	0.03	0.122	3.36
		Bay Anchovy	0	0.134	3.355
		Bayou Topminnow	0.12	0.015	3.186
Cluster 2 vs 5	95.1	Unidentified Sciaenid	0.07	0.786	21.024
		Largemouth Bass	0.431	0	12.392
		Brook Silverside	0.413	0	11.678
		Stripped Mullet	0	0.332	8.501
		Pinfish	0	0.183	5.073
		Redear Sunfish	0.158	0	4.495
		Bluegill	0.14	0	3.911
		Bayou Topminnow	0.12	0	3.195
Cluster 3 vs 4	83.2	Daggerblade Grass Shrimp	0.086	0.753	17.522
		Inland Silverside	0.377	0.122	8.516
		Bay Anchovy	0.314	0.134	8.342
		Spot	0.253	0.076	6.585
		Pinfish	0.208	0.013	4.98
		Unidentified Mullet	0.124	0.061	4.153
		Sheepshead Minnow	0.008	0.126	3.29
		Gulf Killifish	0.024	0.126	3.153
Cluster 3 vs 5	88.2	Unidentified Sciaenid	0.003	0.786	21.518

Comparison	Total dissimilarity	Species	Avg. A	Avg. B	Contribution
Cluster 4 vs 5	86.3	Inland Silverside	0.377	0.057	9.198
		Bay Anchovy	0.314	0	8.397
		Stripped Mullet	0.037	0.332	8.013
		Spot	0.253	0	6.615
		Pinfish	0.208	0.183	5.363
		Unidentified Mullet	0.124	0	3.505
		Daggerblade Grass shrimp	0.086	0.106	3.212
		Unidentified Sciaenid	0.05	0.786	21.329
		Daggerblade Grass shrimp	0.753	0.106	18.901
		Stripped Mullet	0.016	0.332	8.35
		Pinfish	0.013	0.183	4.868
		Sheepshead Minnow	0.126	0.045	3.932
		Gulf Killifish	0.126	0.048	3.54
		Bay Anchovy	0.134	0	3.501
		Inland Silverside	0.122	0.057	3.411

Table 7: Variance explained by both CCA axis and correlations of important species. The CCA analysis was conducted on square root transformed proportional abundance data. All variables included were found to be statistically significant through the use of a permutation routine.

		CCA1	CCA2
Eigenvalues		0.342	0.117
Proportional variance		67.0%	23.0%
Cumulative variance		67.0%	90.0%
<u>Environmental correlations</u>			
Salinity		0.988	0.131
Dissolved Oxygen		-0.238	-0.417
Temperature		-0.167	0.985
<u>Species correlations</u>			
Species Code	Common Name		
REAR	Redear Sunfish	-0.490	-0.203
BLGL	Bluegill	-0.528	-0.098
LGMB	Largemouth Bass	-0.510	-0.271
SGAR	Spotted Gar	-0.521	0.273
GUMH	Gulf Menhaden	-0.384	-0.133
BSVS	Brook Silverside	-0.546	-0.033
ISVS	Inland Silverside	0.446	-0.017
BAYA	Bay Anchovy	0.312	0.198
PINF	Pinfish	0.676	0.570
SPOT	Spot	0.594	0.133
GSHR	Daggerblade Grass Shrimp	0.795	-0.510
GUKF	Gulf Killifish	0.692	-0.438
SMUL	Stripped Mullet	0.218	-0.060
USCI	Sciaenid spp.	1.148	-0.944

Table 8: The 19 prey categories (frequency>1%) contained in Largemouth Bass with food in their stomach. Frequency =number of occurrences/n, mean proportion by weight = total weight (g)/n. Where n = 425, which was the number of Largemouth Bass stomachs that contained one of the 19 prey categories.

Group/Common Name	Frequency	Mean Proportion by Weight
Teleost Fishes		
Bay Anchovy	0.021	1.00
Mosquito Fish	0.016	0.97
Goby	0.040	2.46
Gulf Killifish	0.024	2.02
Gulf Menhaden	0.141	10.68
Inland Silverside	0.031	2.72
Largemouth Bass	0.031	2.45
Rainwater Killifish	0.009	0.94
Striped Mullet	0.012	1.13
Spot	0.014	0.95
Sunfish	0.066	5.51
Blue Crab	0.388	29.30
Salt Marsh Mud Crab	0.238	16.54
Grass Shrimp	0.160	11.39
Mysida Shrimp		
Mysid Shrimp	0.115	8.71
Gastropod Crustaceans		
Neritina	0.026	0.83
Orders of Insecta		
Odonata	0.014	0.72
Hemiptera	0.014	0.70
Amphipoda	0.059	0.96

Table 9: Number of individual Largemouth Bass collected with items in their diet from three sites in Mobile Bay, AL from April, 2011 – March, 2015. Seasons include: Fall = October, spring = March - April, summer = June - August, winter = December – February.

Site	Fall	Spring	Summer	Winter	Total
Bay Minette	22	33	34	119	208
D' Olive Bay	18	51	59	2	130
Fowl River	1	87	28	13	129
Total	41	171	121	134	467

Table 10: Results of the Kruskal-Wallis tests. If the global null hypothesis was rejected, PMCMR was used to confirm group differences. A “*” indicates significance at α =0.05.

Test	Kruskal-Wallis	PMCMR		
Shannon's Diversity:				
Season	0.375			
Site	<0.001*		Bay Minette	D'Olive Bay
		D'Olive Bay	0.98	-
		Fowl River	<0.001*	0.002*
Richness:				
Season	0.330			
Site	<0.001*		Bay Minette	D'Olive Bay
		D'Olive Bay	0.91	-
		Fowl River	<0.001*	0.01*

Table 11: The %PCA analysis on proportional %W data showing prey type abbreviations, eigenvalues, proportional variance explained, and the strength of correlation for each prey type.

		%PCA 1	%PCA 2	%PCA 3	%PCA 4
	Eigenvalues	0.201	0.125	0.098	0.088
	Proportion of total variance explained	0.271	0.168	0.132	0.118
AMPH	Amphipoda	0.008	0.009	0.000	0.016
BAYA	Bay Anchovy	0.010	0.007	0.003	0.009
BLCR	Blue Crab	**-0.928**	-0.094	0.007	-0.058
CORI	Hemiptera	0.006	0.005	0.001	0.005
GAMB	Mosquito Fish	0.010	0.009	-0.001	0.008
GOBY	Goby	0.026	0.026	-0.011	0.007
GSHR	Grass Shrimp	0.154	0.349	**-0.703**	-0.377
GUKF	Gulf Killifish	0.021	0.011	-0.002	0.011
GUMH	Gulf Menhaden	0.178	0.250	**0.705**	-0.441
ISVS	Inland Silverside	0.027	0.022	0.007	0.018
LGMB	Largemouth Bass	0.022	0.014	0.003	0.018
MUDC	Salt Marsh Mud Crab	0.245	**-0.877**	-0.070	-0.099
MYSH	Mysid Shrimp	0.126	0.180	0.049	**0.803**
NERI	Neritinia	-0.002	0.001	0.001	0.001
ODON	Odonata	0.007	0.005	0.001	0.005
RWKF	Rainwater Killifish	0.009	0.007	0.001	0.006
SMUL	Striped Mullet	0.010	0.008	0.000	0.006
SPOT	Spot	0.010	0.005	0.008	0.000
SUNF	Sunfish	0.061	0.062	0.001	0.062

Figure 1: Map showing the study sites sampled in the Mobile Bay estuary, Alabama, USA, including sampled sites from upstream to downstream (Bay Minette, D' Olive Bay, Fowl River North, Fowl River, Fowl River South, Fowl Bay A, Fowl Bay B, Wolf Bay, Perdido Bay).

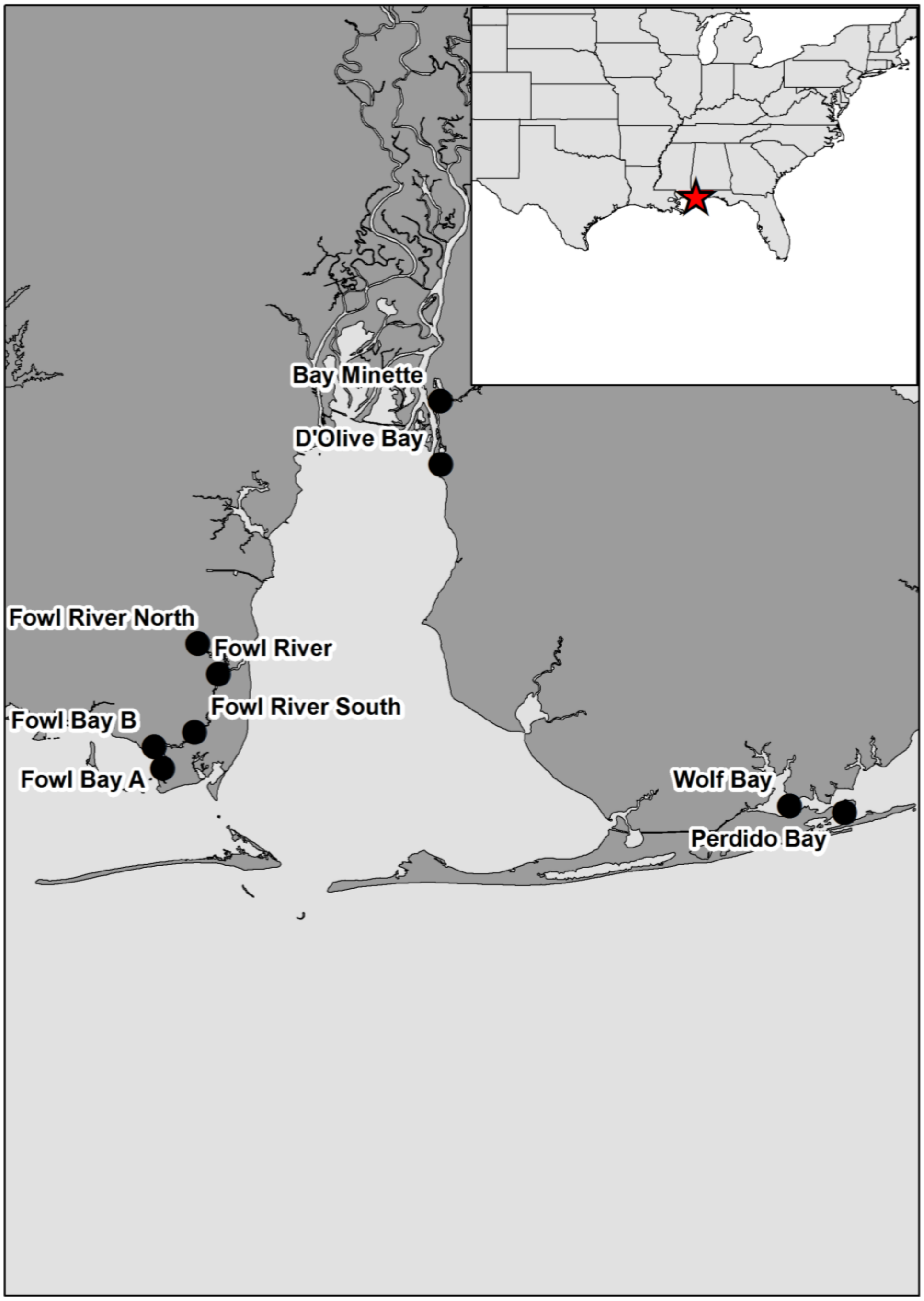
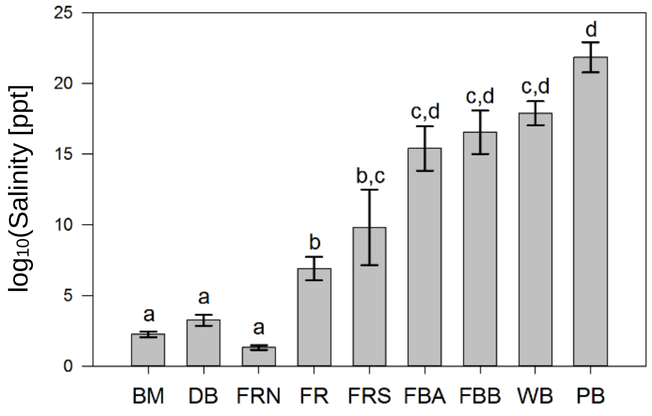
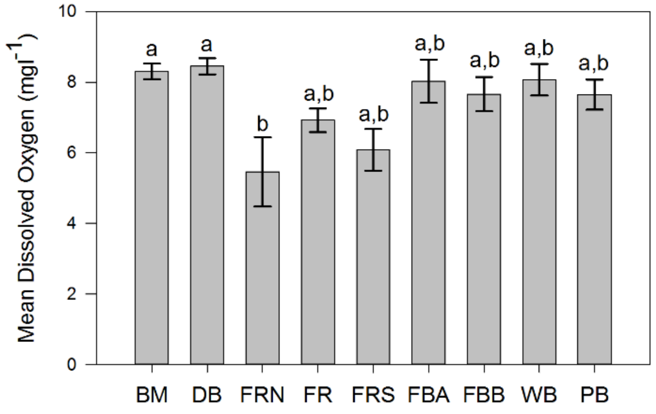

Bay Minette
D'Olive Bay
Fowl River North
Fowl River
Fowl River South
Fowl Bay B
Fowl Bay A
Wolf Bay
Perdido Bay

Figure 2: Spatial variation in mean salinity (ppt) (measured just below the surface), dissolved oxygen (mg^{-l}), and water temperature (ºC) (error bars +/- SE). Sites are arranged from upstream (left) to downstream (right) and site abbreviations are as defined in Table 1. Bars with different letters indicate statistical differences ($\alpha = 0.05$) based upon Tukey’s Honest Significant Differences.


log10(Salinity [ppt]
0
5
10
15
20
25
a
a
a
b
b,c
c,d
c,d
c,d
d
BM
DB
FRN
FR
FRS
FBA
FBB
WB
PB


Mean Dissolved Oxygen (mgl-1)
0
2
4
6
8
10
a
a
b
a,b
a,b
a,b
a,b
a,b
a,b
BM
DB
FRN
FR
FRS
FBA
FBB
WB
PB

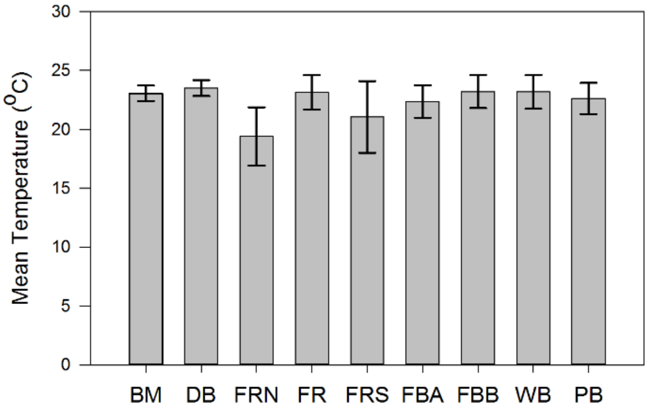
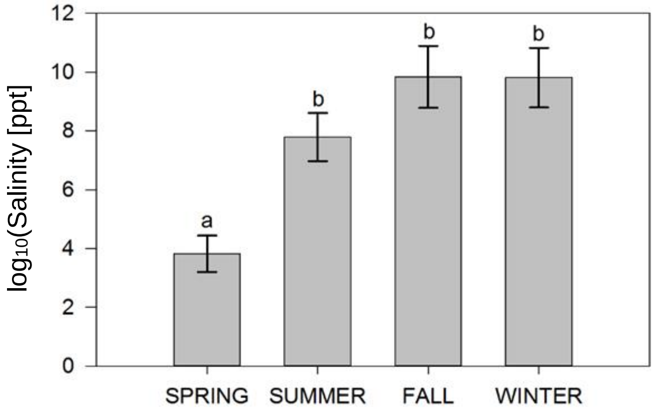
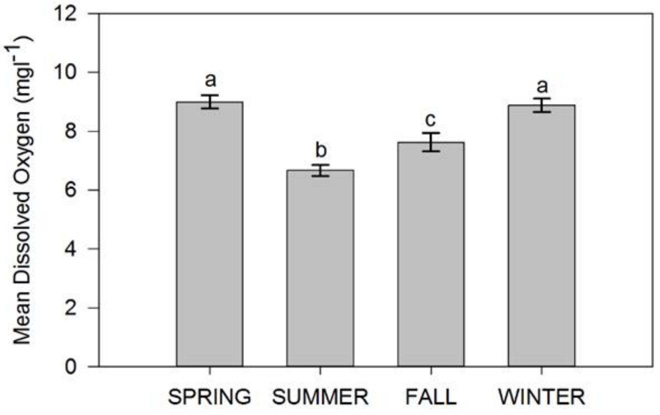

Mean Temperature (oC)
0
5
10
15
20
25
30
BM
DB
FRN
FR
FRS
FBA
FBB
WB
PB

Figure 3: Seasonal variation in mean surface salinity, dissolved oxygen, and water temperature (error bars +/- SE). Where SPRING = March – May, SUMMER = June – August, FALL = September – November, WINTER = December – February. Bars with different letters indicate statistical differences ($\alpha = 0.05$) based upon Tukey's Honest Significant Differences.


log10(Salinity [ppt]
12
10
8
6
4
2
0
a
b
b
b
SPRING
SUMMER
FALL
WINTER


Mean Dissolved Oxygen (mgl-1)
12
10
8
6
4
2
0
a
b
c
a
SPRING
SUMMER
FALL
WINTER

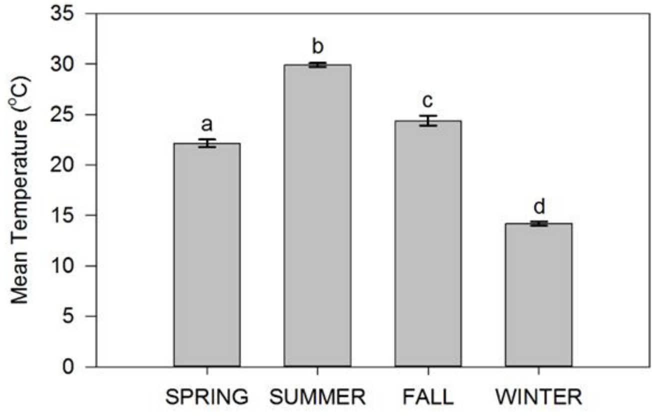

Mean Temperature (°C)
35
30
25
20
15
10
5
0
a
b
c
d
SPRING
SUMMER
FALL
WINTER

Figure 4: Graphs of nMDS results showing sampling events in species space. Shapes/colors indicate cluster membership as identified by hierarchical clustering using the group averaging linkage method on a similarity matrix of Bray - Curtis values.

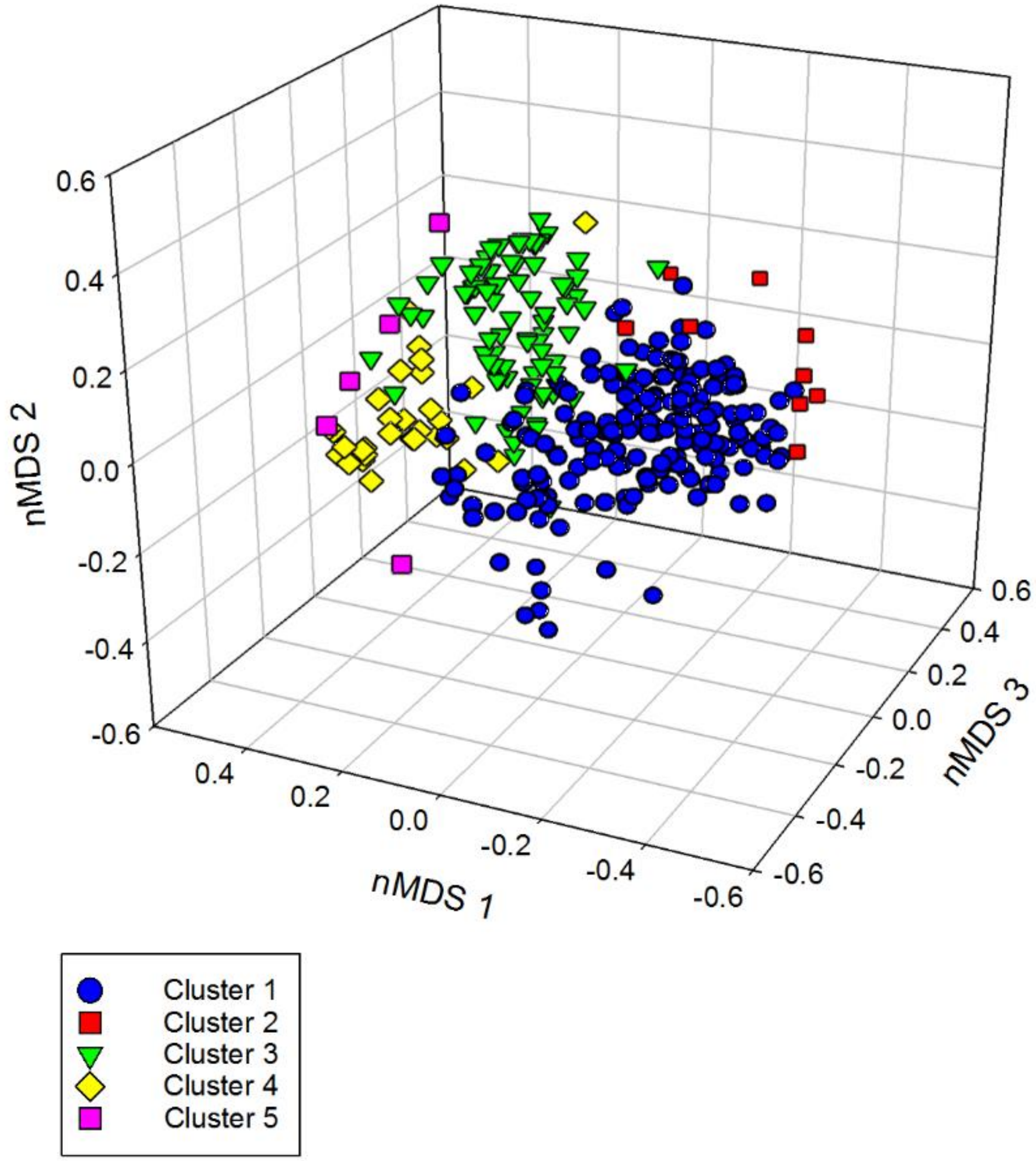

nMDS 2
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
nMDS 1
0.4
0.2
0.0
-0.2
-0.4
-0.6
nMDS 3
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
● Cluster 1
■ Cluster 2
▼ Cluster 3
◆ Cluster 4
■ Cluster 5

Figure 5: Graphs of CCA ordinations showing the first and second axes that explained 67.0% and 23.0% of the species-environmental relationship. (A) Species positions are overlaid as weighted averages of the proportional abundance within the community data matrix. Species abbreviations are as defined in Table 7. Vector arrows represent environmental variables and the length is the relative the strength of the correlation with the CCA axis. (B) Positions of the mean CCA scores calculated by site. Bi-directional error bars represent 1SD from the mean CCA score of a respective sample site.

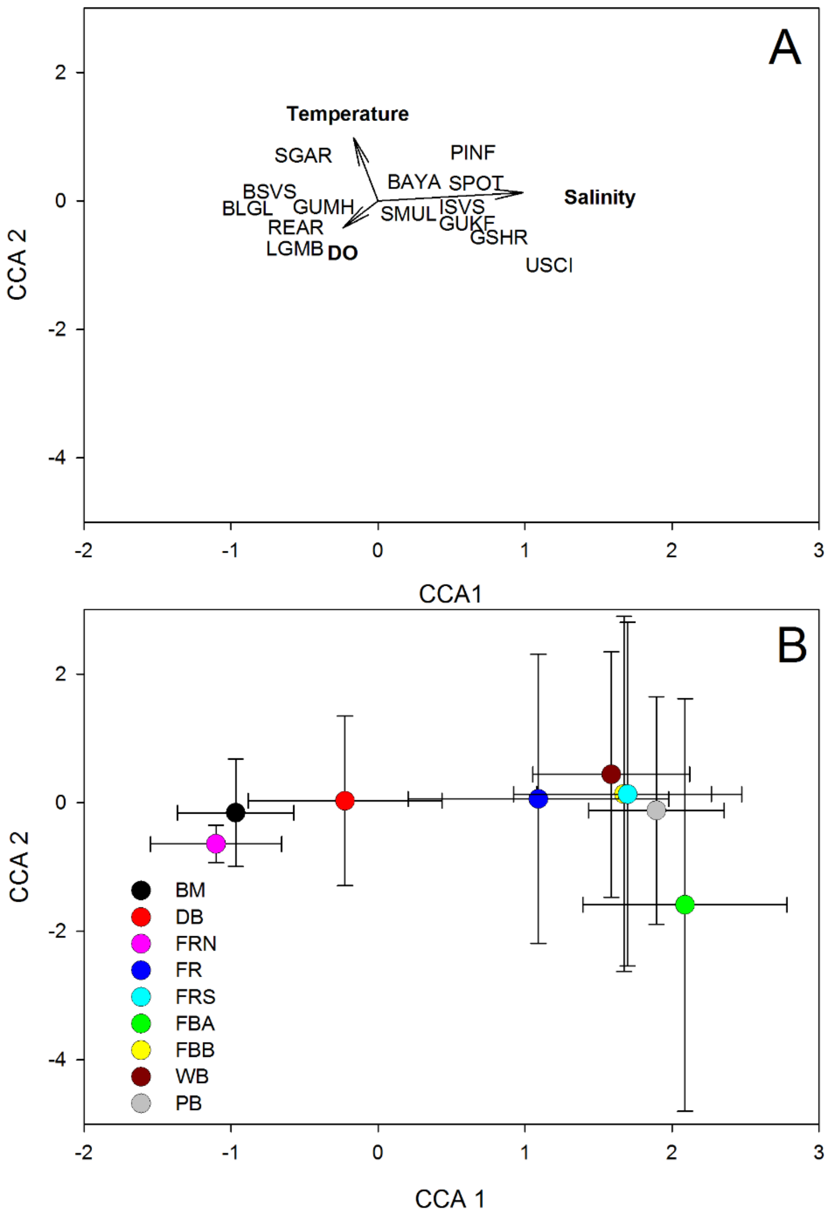

A
Temperature
SGAR
PINF
BAYA
SPOT
Salinity
BSVS
BLGL
GUMH
SMUL
ISVS
GUKF
GSHR
REAR
LGMB
DO
USCI
CCA 2
CCA1
2
0
-2
-4
-2
-1
0
1
2
3
B
● BM
● DB
● FRN
● FR
● FRS
● FBA
● FBB
● WB
● PB
CCA 2
CCA 1

Figure 6: A map of the study area indicating the three sample sites used for fish collections in Mobile Bay, Alabama.

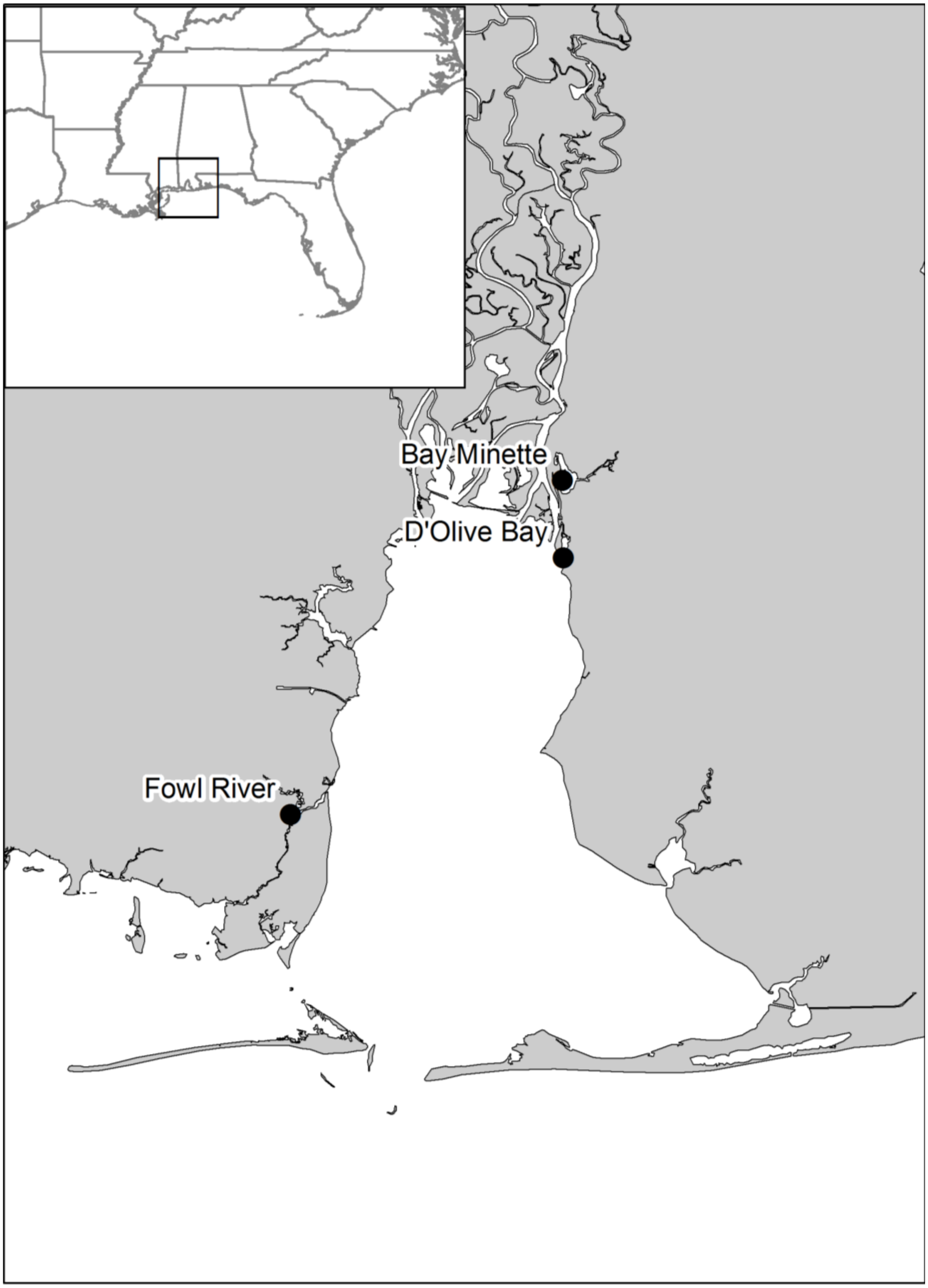

Bay Minette
D'Olive Bay
Fowl River

Figure 7: Bi-monthly surface salinity values recorded at each sampling event throughout the study period.

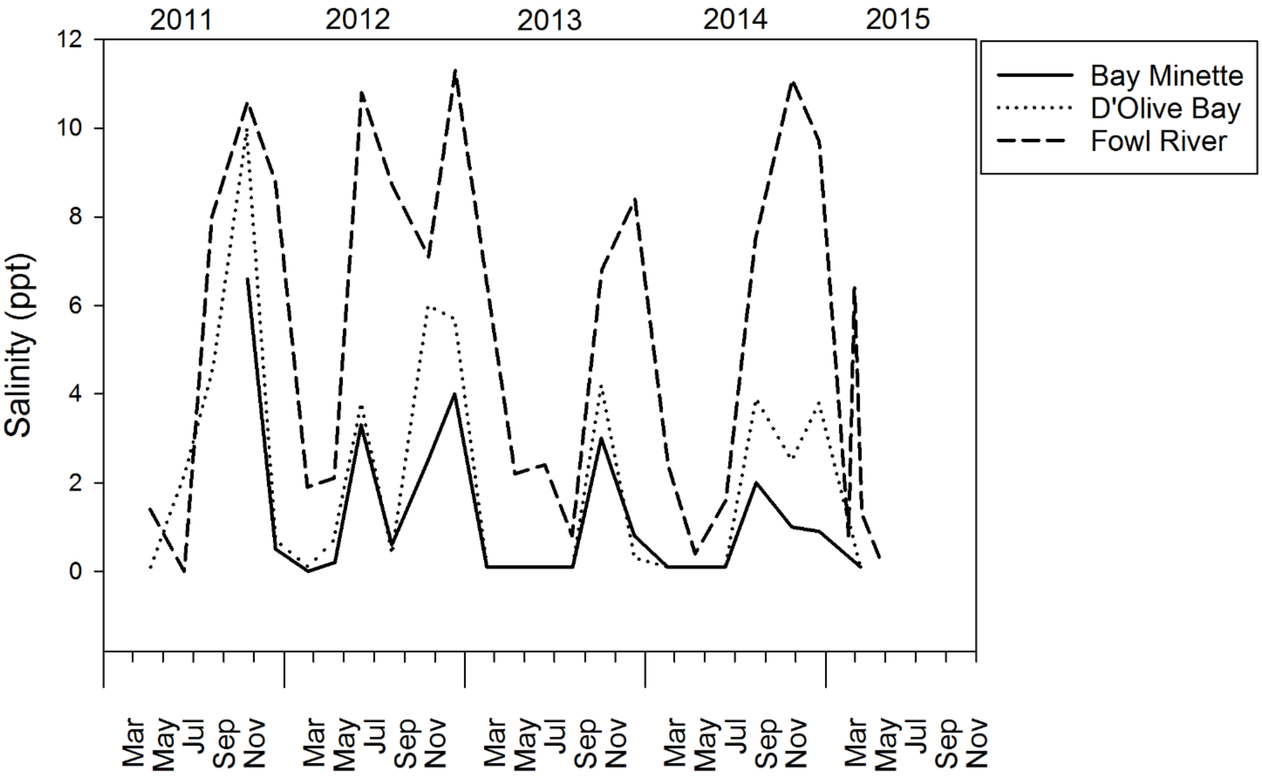

2011
2012
2013
2014
2015
Salinity (ppt)
12
10
8
6
4
2
0
Mar
May
Jul
Sep
Nov
Mar
May
Jul
Sep
Nov
Mar
May
Jul
Sep
Nov
Mar
May
Jul
Sep
Nov
Mar
May
Jul
Sep
Nov
Bay Minette
D'Olive Bay
Fowl River

Figure 8: Length-frequency histograms showing the number of fish of each size captured at each of the three study sites

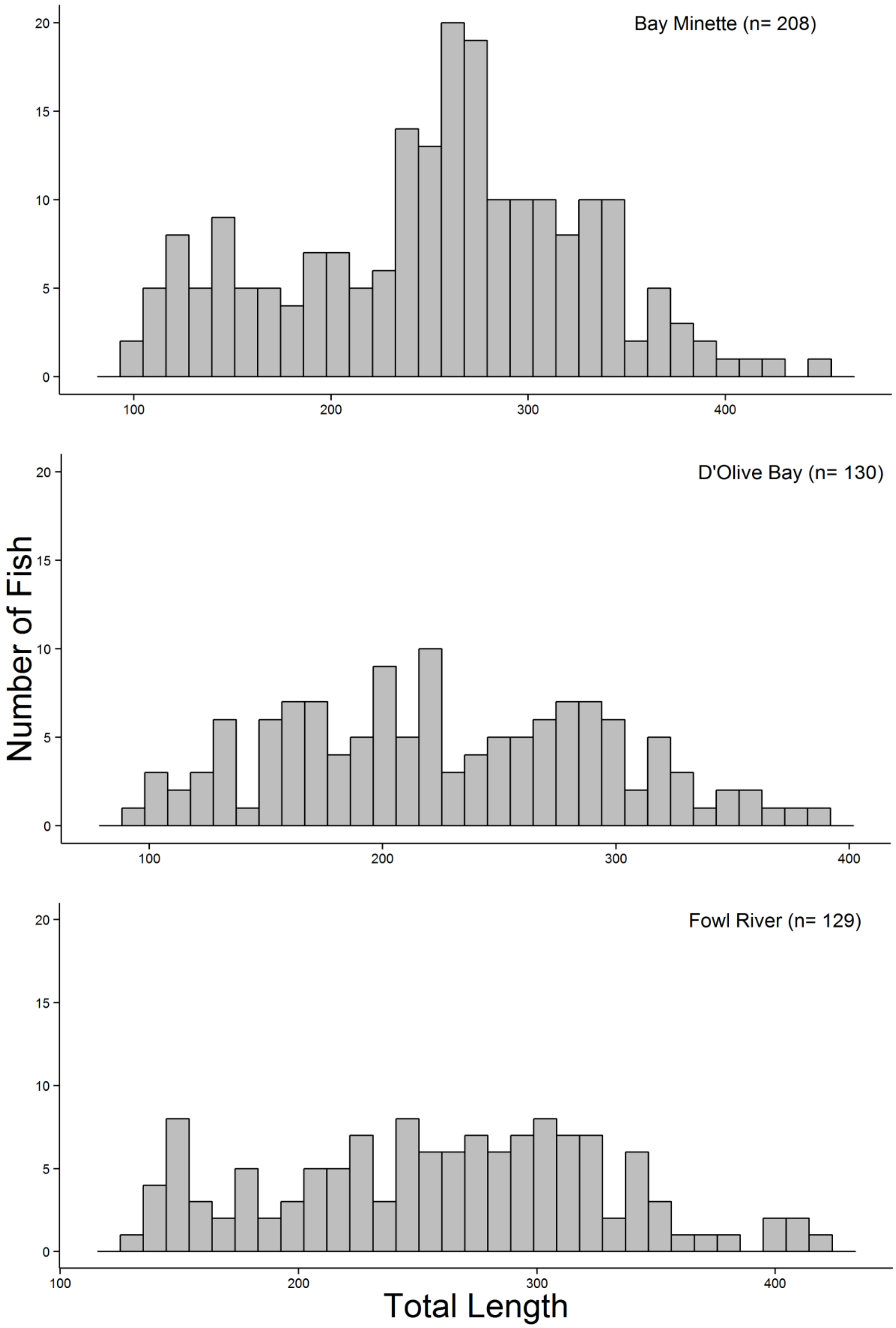
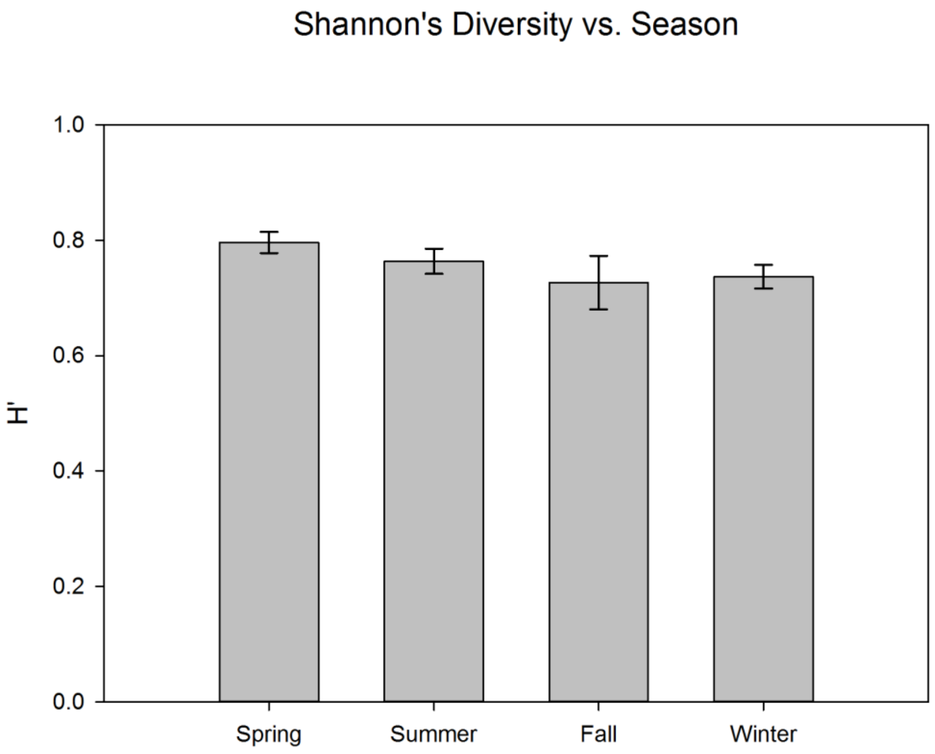

Bay Minette (n= 208)
D'Olive Bay (n= 130)
Fowl River (n= 129)
Number of Fish
Total Length
0
5
10
15
20
100
200
300
400

Figure 9: Mean Shannon's diversity index calculated across season and sites (error bars +/- SE).


Shannon's Diversity vs. Season
H'
1.0
0.8
0.6
0.4
0.2
0.0
Spring
Summer
Fall
Winter

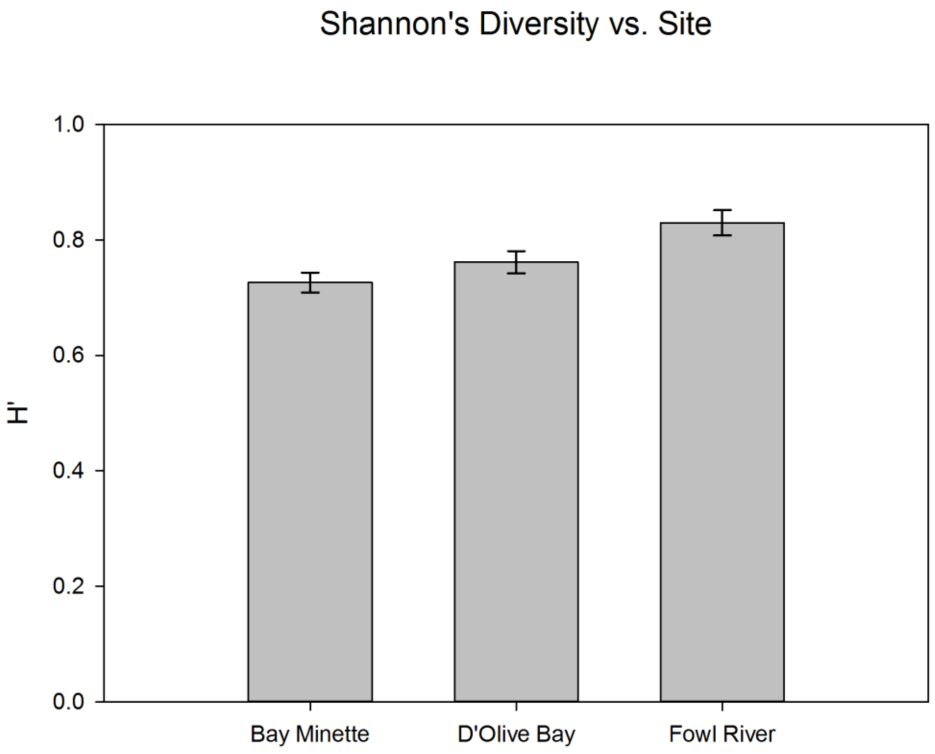
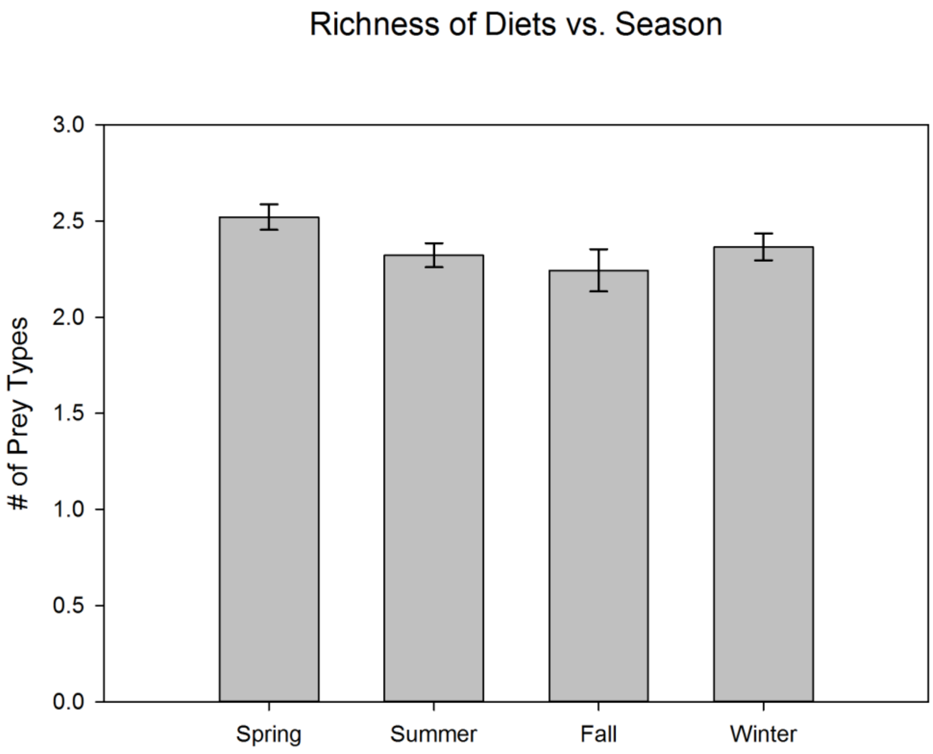

Shannon's Diversity vs. Site
H'
1.0
0.8
0.6
0.4
0.2
0.0
Bay Minette
D'Olive Bay
Fowl River

Figure 10: Mean diet richness calculated across season and site (error bars +/- SE).


Richness of Diets vs. Season
# of Prey Types
3.0
2.5
2.0
1.5
1.0
0.5
0.0
Spring
Summer
Fall
Winter

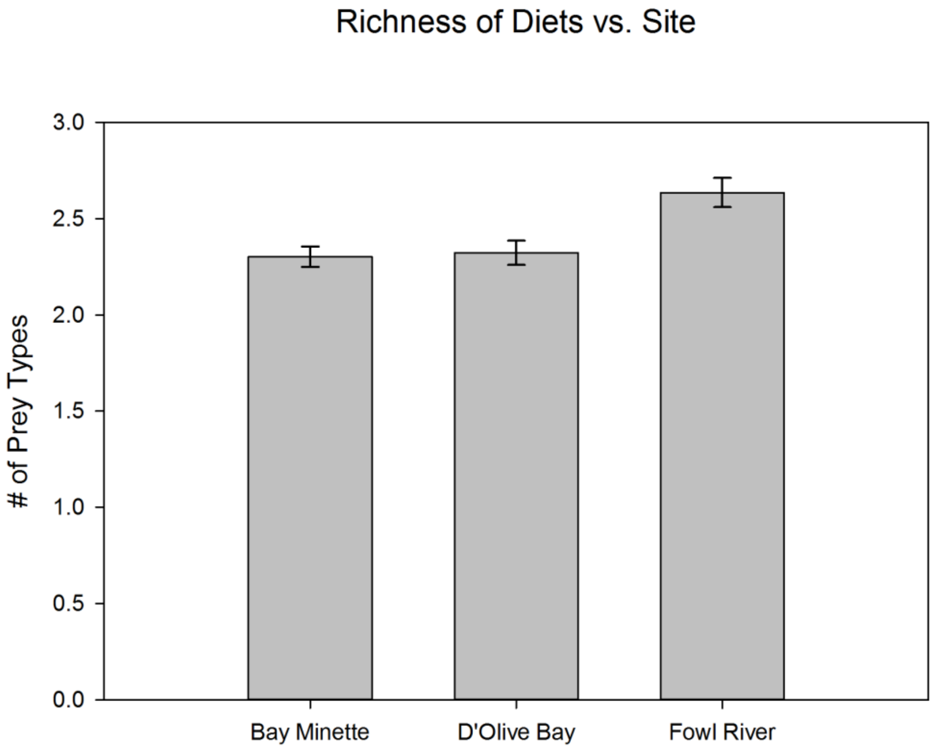

Richness of Diets vs. Site
# of Prey Types
3.0
2.5
2.0
1.5
1.0
0.5
0.0
Bay Minette
D'Olive Bay
Fowl River

Figure 11: The first two %PCA axes showing the diet dissimilarities based upon proportional weight of prey items in stomachs. %PCA 1 explained 27.1% variation within the data. %PCA 2 explained 16.8% of the variation within the data. (A) Shows individual diet positions overlaid with prey category vectors, only 6 prey categories were plotted for visual clarity (B) Shows mean site scores overlaid with prey category vectors (error bars = 1SD). Species Abbreviations are found in Table 11.

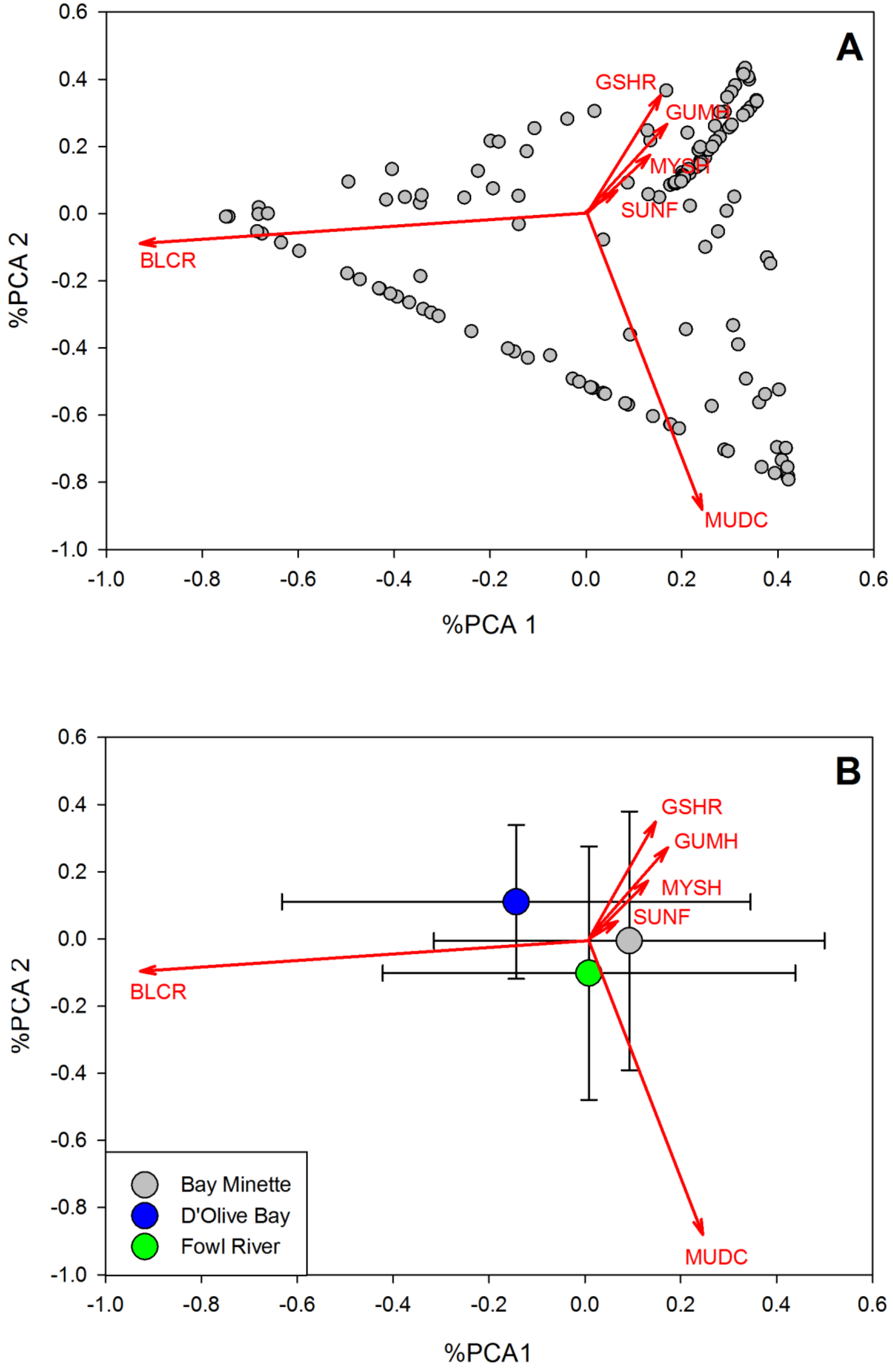
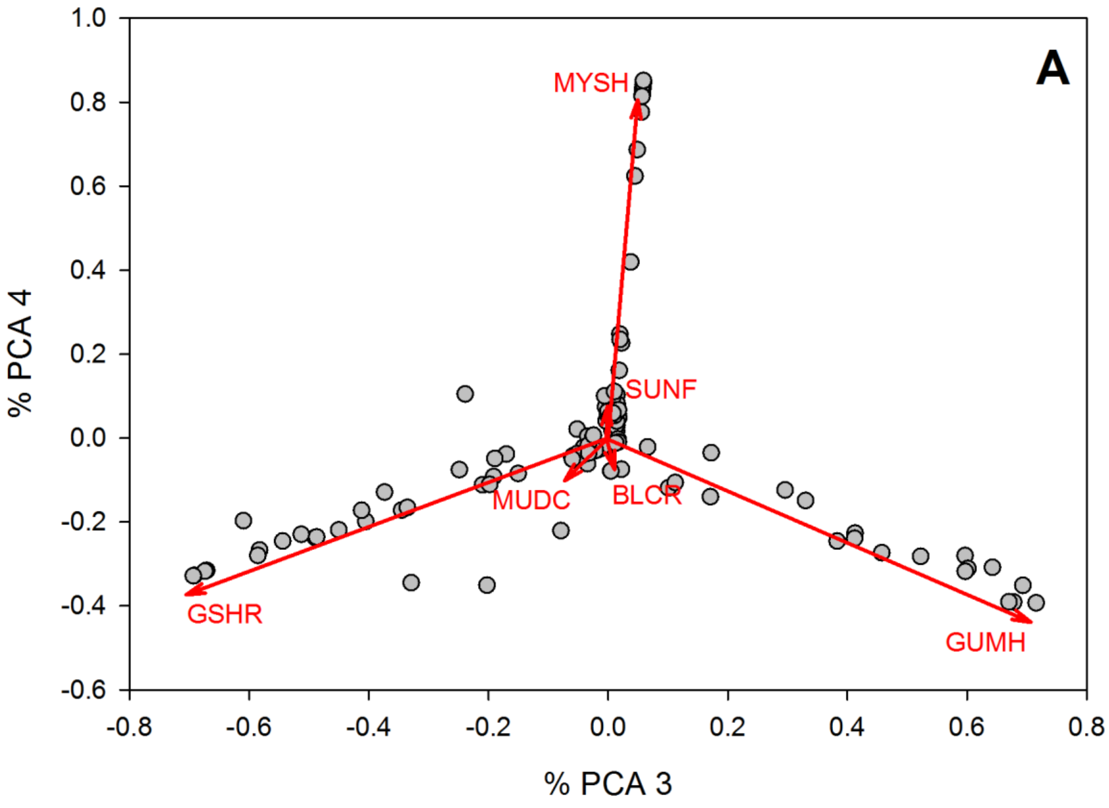

A
B
%PCA 1
%PCA1
%PCA 2
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
-1.0
GSHR
GUMH
MYSH
SUNF
BLCR
MUDC
Bay Minette
D'Olive Bay
Fowl River

Figure 12: The third and fourth %PCA axes showing the diet dissimilarities based upon proportional weight of prey items in stomachs. %PCA 3 explained 13.2% variation within the data. %PCA 4 explained 11.8% of the variation within the data. (A) Shows individual diet positions overlaid with prey category vectors only 6 prey categories were plotted for visual clarity. (B) Shows mean site scores overlaid with prey category vectors (error bars = 1SD). Species Abbreviations are found in Table 11.


A
MYSH
SUNF
MUDC
BLCR
GSHR
GUMH
% PCA 4
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
-0.6
-0.4
-0.2
0.0
0.2
0.4
0.6
0.8
% PCA 3

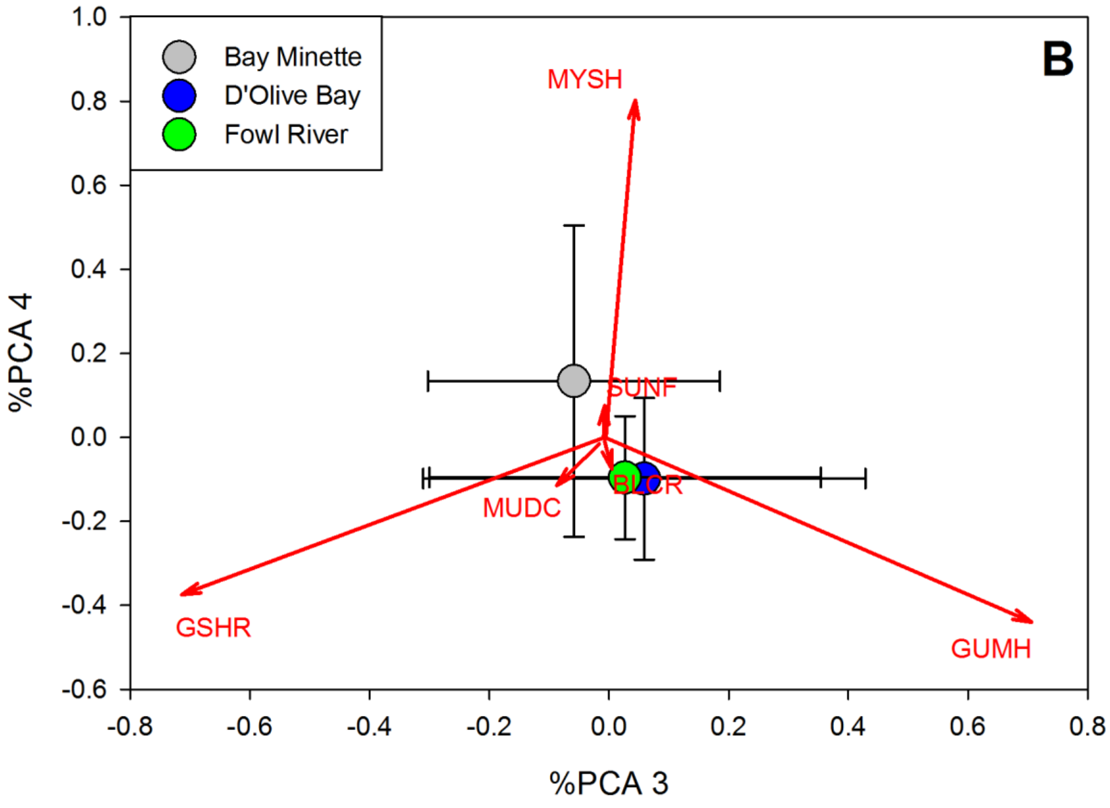
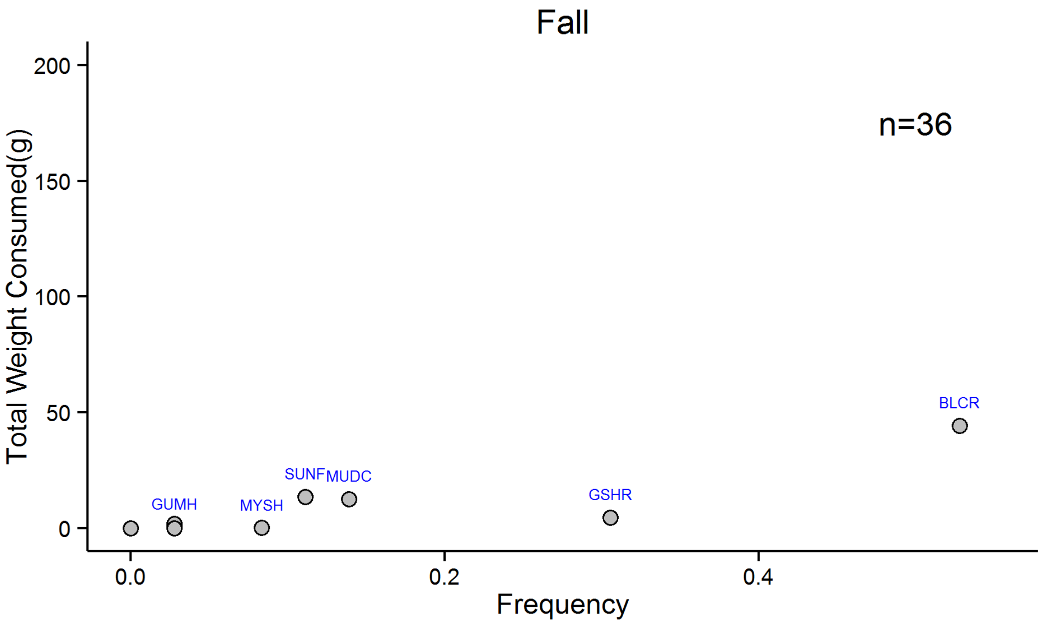

B
Bay Minette
D'Olive Bay
Fowl River
MYSH
SUNF
MUDC
BLCR
GSHR
GUMH
%PCA 4
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
-0.6
-0.4
-0.2
0.0
0.2
0.4
0.6
0.8
%PCA 3

Figure 13: Fall and spring diets showing the abundance of 19 prey types. The y axis = total prey weight consumed (g), x axis = frequency of occurrence across fish with items in their diet. Prey categories identified as important by %PCA analysis are labeled.


Fall
n=36
Total Weight Consumed(g)
200
150
100
50
0
Frequency
0.0
0.2
0.4
BLCR
SUNF
MUDC
GUMH
MYSH
GSHR

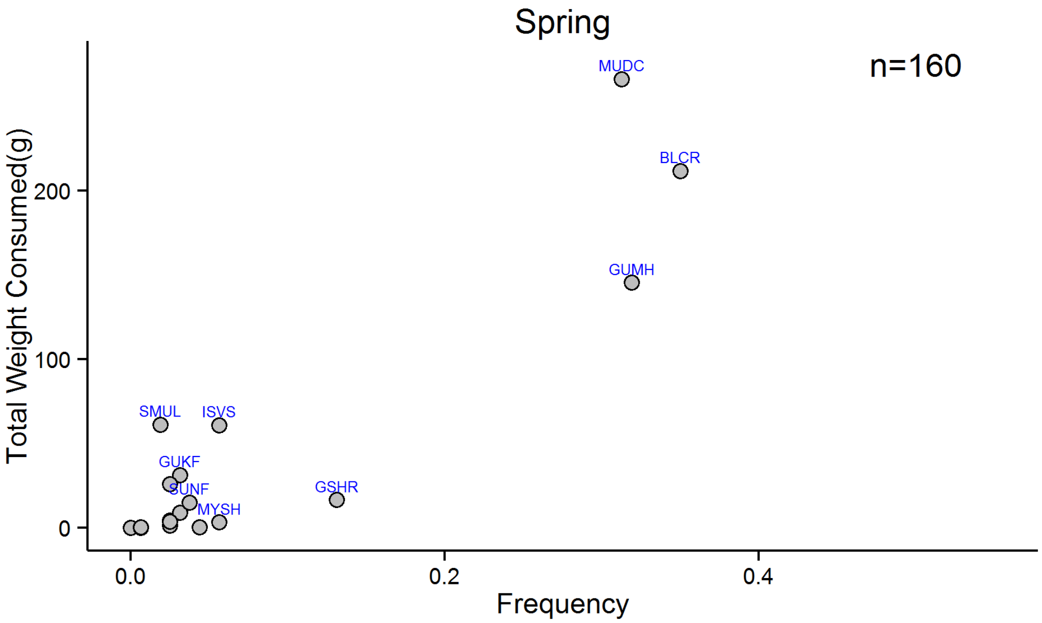
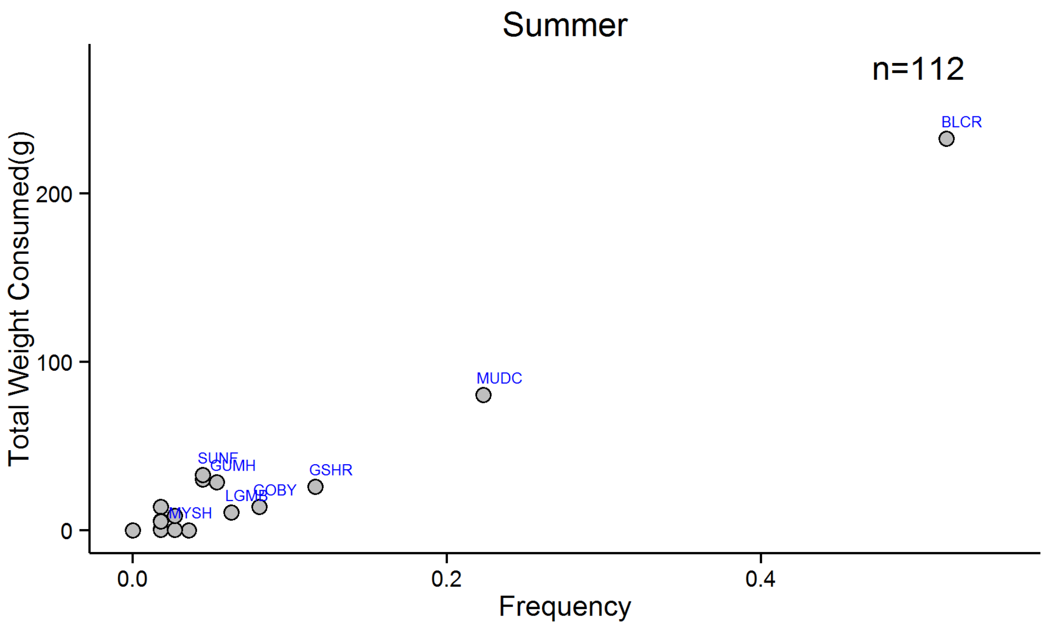

Spring
n=160
Total Weight Consumed(g)
200
100
0
Frequency
0.0
0.2
0.4
MUDC
BLCR
GUMH
SMUL
ISVS
GUKF
SUNF
MYSH
GSHR

Figure 14: Summer and winter diets showing the abundance of 19 prey types. The y axis = total prey weight consumed (g), x axis = frequency of occurrence across fish with items in their diet. Prey categories identified as important by %PCA analysis are labeled.


Summer

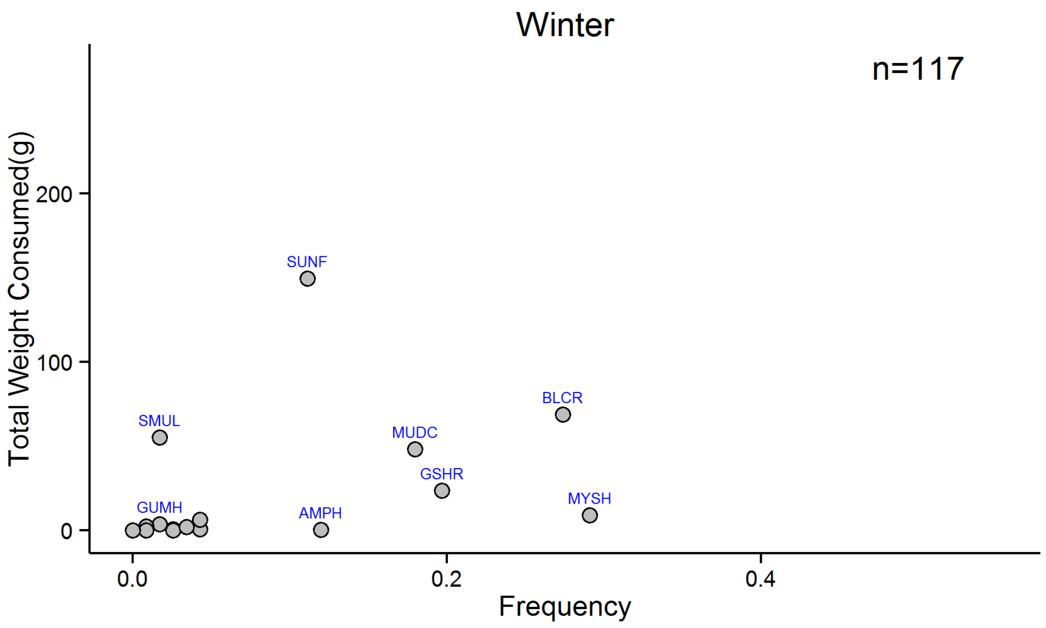
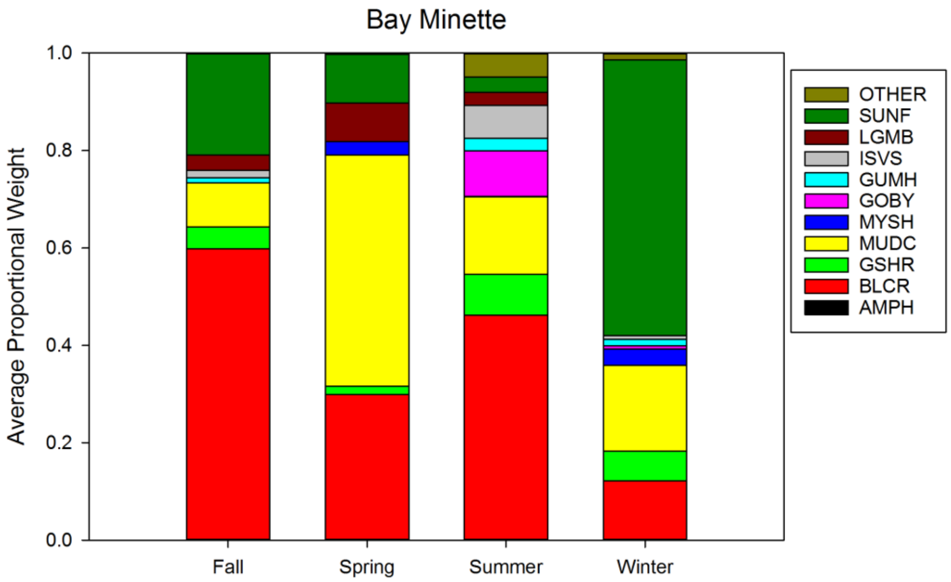
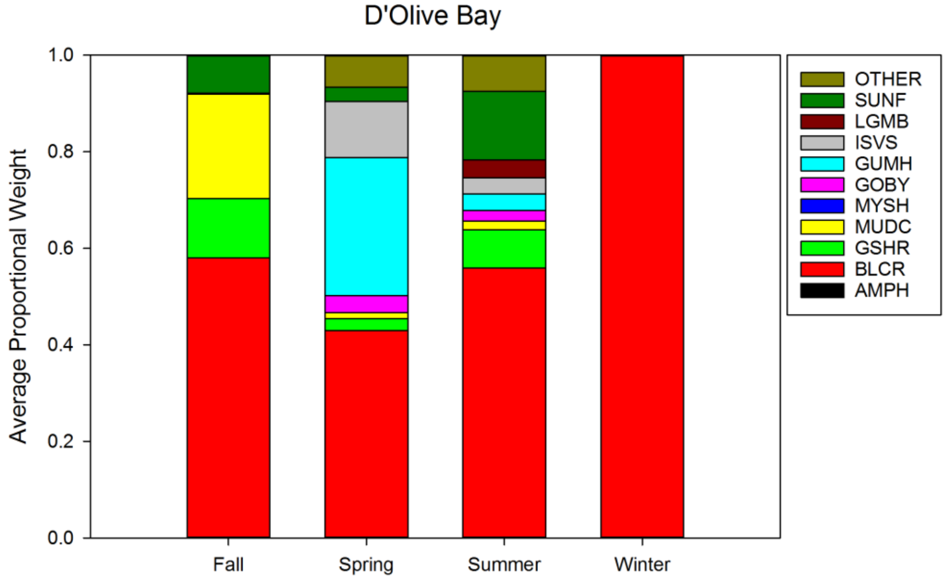
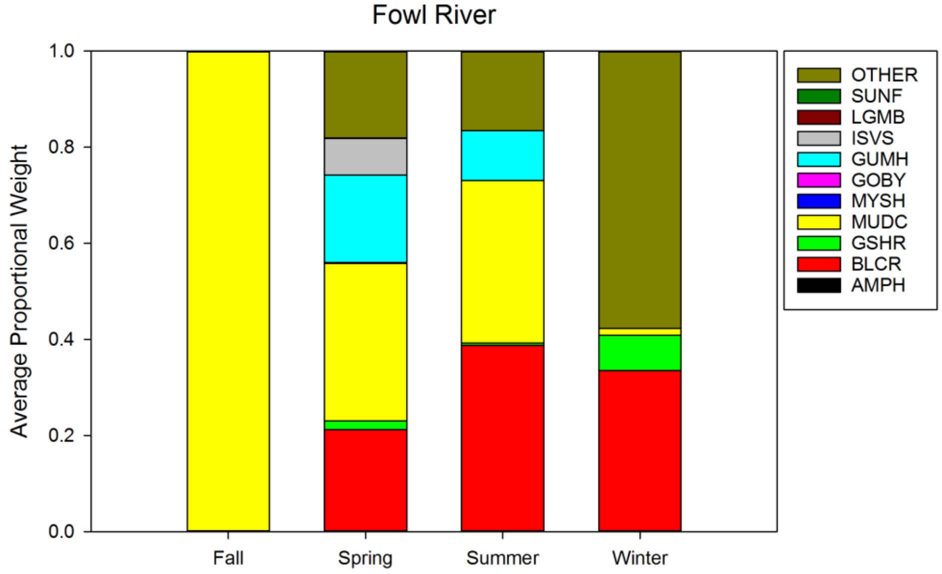

Winter

Figure 15: Average proportional weight across site and season. D’Olive Bay-winter (n=2) and Fowl River-fall (n=1) represent very small numbers of diets.


Bay Minette
Average Proportional Weight
1.0
0.8
0.6
0.4
0.2
0.0
Fall
Spring
Summer
Winter
OTHER
SUNF
LGMB
ISVS
GUMH
GOBY
MYSH
MUDC
GSHR
BLCR
AMPH


D'Olive Bay
Average Proportional Weight
1.0
0.8
0.6
0.4
0.2
0.0
Fall
Spring
Summer
Winter
OTHER
SUNF
LGMB
ISVS
GUMH
GOBY
MYSH
MUDC
GSHR
BLCR
AMPH


Fowl River
Average Proportional Weight
1.0
0.8
0.6
0.4
0.2
0.0
Fall
Spring
Summer
Winter
OTHER
SUNF
LGMB
ISVS
GUMH
GOBY
MYSH
MUDC
GSHR
BLCR
AMPH